# Article

# Revision of the horseface loaches (Cobitidae, *Acantopsis*), with descriptions of three new species from Southeast Asia

DAVID A. BOYD[1,8], PATCHARA NITHIROJPAKDEE[2], GRIDSADA DEEIN[3], CHAVALIT VIDTHAYANON[4], CHAIWUT GRUDPAN[5], WEERAPONGSE TANGJITJAROEN[6], JOHN M. PFEIFFER[1], ZACHARY S. RANDALL[1], TIPPAMAS SRISOMBAT[7] & LAWRENCE M. PAGE[1,8]

[1]*Florida Museum of Natural History, University of Florida, Gainesville, Florida, 32611, USA.*
[2]*Faculty of Agro-Industrial Technology, Rajamangala University of Technology, Tawan-Ok Chanthaburi Campus, Chanthaburi Thailand*
[3]*Suphan Buri Inland Fisheries Research and Development Center, Mueang District, Suphan Buri 72000 Thailand*
[4]*Independent Researcher, Bangkok, Thailand*
[5]*Department of Fisheries, Faculty of Agriculture, Ubonrajathanee University, Thailand*
[6]*Faculty of Veterinary Medicine, Chiang Mai University, Chiang Mai 50100 Thailand*
[7]*Inland Fisheries Research and Development Division, Department of Fisheries, Kasetklang, Chatuchak, Bangkok 10900 Thailand*
[8]*Corresponding author. E-mail: dboyd@flmnh.ufl.edu, L.M. Page: lpage1@ufl.edu*

## Abstract

*Acantopsis* (Cobitidae) is revised based on analysis of morphological and molecular data. Four of the six available names, *A. dialuzona, A. spectabilis, A. octoactinotos,* and *A. thiemmedhi*, are valid, and three new species, *A. rungthipae, A. dinema,* and *A. ioa*, are described. All species are described morphologically, distributions are mapped, and relationships are discussed for those for which molecular data (*CO1, RAG1*) are available. Labial barbels, color pattern, and meristic counts are the most diagnostic features. Although the long snout of *Acantopsis* is perhaps the most emblematic attribute of the genus, its relative length increases with growth, reducing its taxonomic value. Species can be difficult to identify on the basis of color pattern alone, as habitat and preservation methods appear to strongly influence the color pattern. Despite interspecific overlap of some highly variable traits, each species has a unique set of morphological characteristics that remain observable even when the color pattern is obscured, and some species are restricted to single drainages, greatly simplifying identification. The phylogenetic analyses revealed high molecular divergence between even the most morphologically similar species, with mean uncorrected *CO1* p-distances between species ranging from 12.1–15.4%. Species of *Acantopsis* exhibit significant genetic structuring consistent with recognized freshwater ecoregions. *Acanthopsis lachnostoma* Rutter 1897, from Swatow, China, is not assignable to *Acantopsis*.

**Key words:** Thailand, Cambodia, Malaysia, Myanmar, Cypriniformes, Cobitoidea

## Introduction

Species of *Acantopsis* (Cobitidae), fishes with the English name of horse-face loaches and known in Thailand and other Southeast Asian countries as banana-root fishes, range from eastern India to Laos, Cambodia, and Vietnam, and south to Borneo and Java. They show considerable morphological variation in color pattern, development of labial barbels, and body shape, but have received surprisingly little attention by systematists. Only six available scientific names have been assigned to *Acantopsis* (Kottelat 2012, Eschmeyer *et al*. 2016): *Acantopsis dialuzona* van Hasselt 1823, described from Jakarta, Java; *Cobitis choirorhynchos* Bleeker 1854, described from southern Sumatra; *Prostheacanthus spectabilis* Blyth 1860, described from Tenasserim provinces, Myanmar; *Acantopsis octoactinotos* Siebert 1991, described from Sabah, Borneo; *Acantopsis thiemmedhi* Sontirat 1999, described from Uthai Thani, Thailand; and *Acantopsis multistigmatus* Vishwanath and Laisram 2005, described from Manipur, India. Of these, Kottelat (2012) recognized *A. dialuzona, A. spectabilis, A. octoactinotos,* and *A. thiemmedhi* as valid names of species. Herein, morphological data on 175 specimens and molecular data on 111 specimens are

analyzed. All available names except *A. choirorhynchos* and *A. multistigmatus* are recognized as those of valid species, and three new species from mainland Southeast Asia are described. Previously described species are rediagnosed based on examination of available types, other preserved specimens, and data from original descriptions.

## Materials and methods

Fieldwork was conducted in Cambodia, Laos, Thailand, and Sumatra using seines, dipnets, and backpack electroshockers where permitted. Specimens were euthanized in MS-222, preserved in 10% formalin, and transferred to 70% ethanol for storage. Photographs of living and preserved specimens were taken with a Canon 7D camera and edited using Adobe Photoshop CS6. A Visionary Digital camera system (Palmyra, Virginia) using the stacking software Helicone Focus was utilized for macro imaging of the mouth. Geographic coordinates were determined using maps and Google Earth. Maps were constructed using ArcMap 10.2.2 in ArcGIS.

**Morphological data.** Meristic and morphometric data were taken on 175 specimens. Primary types were examined for all nominal species of *Acantopsis* with the exception of *A. multistigmatus* Vishwanath and Laisram, which is held at MUMF and unavailable for examination, and *A. spectabilis* Blyth, for which types are unknown or possibly at ZSI but cannot be located (L. Kosygin, pers. comm., 6 Feb. 2017). All morphometric data were taken on the left side when possible, and measurements and counts follow Hubbs and Lagler (2004) except for the following: body depth and body width were measured at the origin of the dorsal fin, and prepectoral, prepelvic, and preanal lengths were taken from the tip of the snout to the base of the first ray of each fin. In measuring caudal-peduncle and anal-fin base lengths, the posterior end of the anal-fin base was the insertion point of the last anal ray, and not the position at which the last membrane contacts the body. Origin and insertion refer to the anterior and posterior points, respectively, at which a median fin connects to the body. All fin lengths were taken with fins depressed. All measurements were taken to the nearest 0.1 mm using dial calipers. Morphometrics are expressed as percentage of standard length (SL) and head length (HL); TL represents total length. The posterior-most element of the last branched ray of the dorsal and anal fins is given as ½ (Kottelat 1990). Counts of vertebrae were made on micro-CT scans or radiographs following the terminology of Roberts (1989), with the first caudal vertebra being the first one with its hemal spine posterior to the anteriormost anal fin pterigiophore, counts of abdominal vertebrae including the Weberian complex (N=4 vertebrae), and counts of caudal vertebrae including the urostyle complex. Dorsal saddle count was taken posterior to the opercle. Lateral blotch count was taken along the length of the body and includes the blotch at the caudal-fin base, when present.

All species of *Acantopsis* have one pair each of unbranched rostral, maxillary, and mandibular barbels. In contrast, labial barbels may be branched or unbranched and vary in their perforation of the medial flap (labium) of the lower lip. A branch, or an entire unbranched barbel, may remain enclosed within the labium, or may perforate the labium and be exposed externally. The externally exposed branches and unbranched barbels are referred to herein as the labial barbels (Fig. 1). Barbels and labial branches are distinguished from papillae on the labium and elsewhere on the mouth by being at least twice as long as the longest papilla.

Specimens examined, listed in Appendix A, were from the following institutions (abbreviations follow Fricke and Eschmeyer, 2016): American Museum of Natural History (AMNH), New York, U.S.A.; Academy of Natural Sciences (ANSP), Philadelphia, U.S.A.; Auburn University Natural History Museum (AUM), Auburn, U.S.A.; Natural History Museum (BMNH), London, U.K.; California Academy of Sciences (CAS), San Francisco, U.S.A.; Field Museum of Natural History (FMNH), Chicago, U.S.A.; Kasetsart University, Museum of Fisheries (KUMF), Bangkok, Thailand; Museum of Comparative Zoology, Harvard University (MCZ), Cambridge, U.S.A.; National Inland Fisheries Institute, Department of Fisheries (NIFI), Bangkok, Thailand; Research Laboratory of Ichthyology, Kasetsart University, (RLIKU); Bangkok, Thailand; National Science Museum (THNHM-F), Pathumthani, Thailand; Naturalis Biodiversity Center (RMNH), Leiden, Netherlands; Florida Museum of Natural History (UF), Gainesville, U.S.A.; University of Michigan Museum of Zoology (UMMZ), Ann Arbor, U.S.A.; Smithsonian Institution National Museum of Natural History (USNM), Washington D.C., U.S.A; Lee Kong Chian Natural History Museum, Singapore (ZRC). Common (vernacular) names are coined herein.
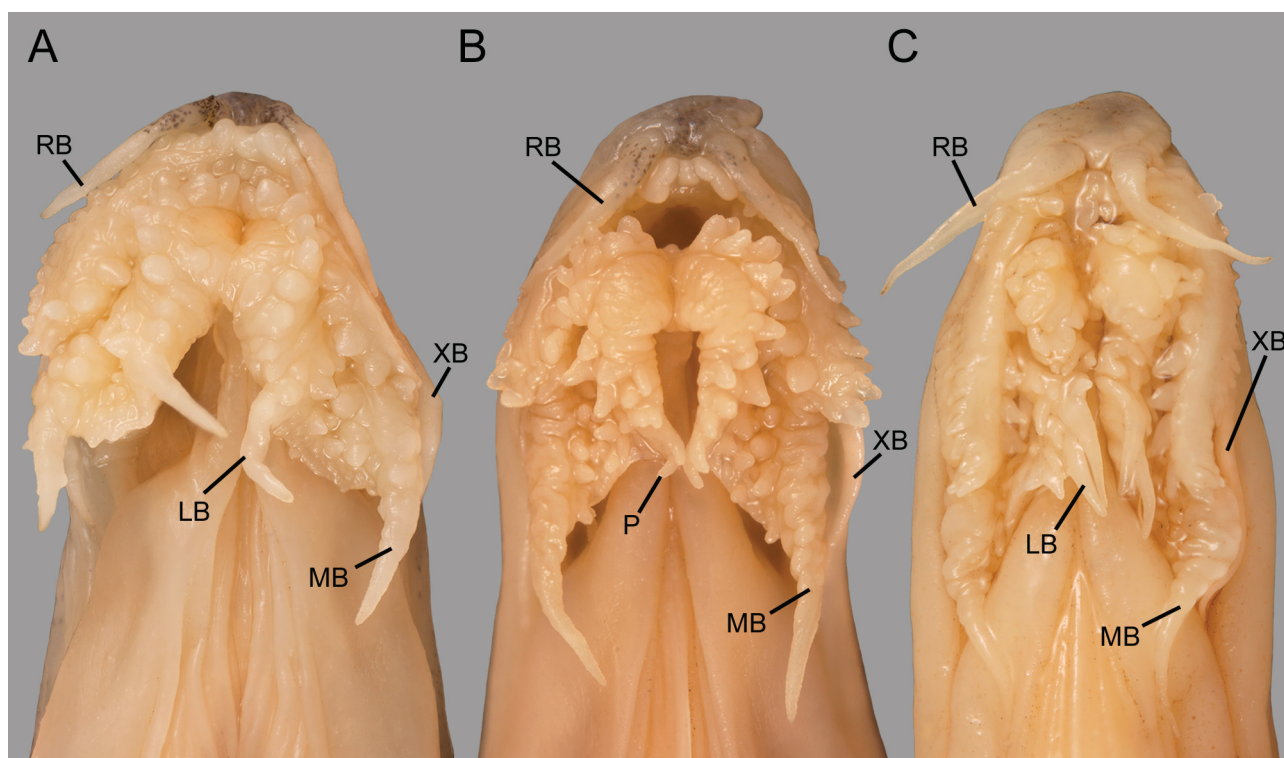
**FIGURE 1.** Mouths of *Acantopsis*. (A) *A. thiemmedhi*, UF 188118, 107.5 mm SL, with one pair of labial barbels. (B) *A. rungthipae*, THNHM F0013610, holotype, 107.4 mm SL (ex. UF 235976), without labial barbels. (C) *Acantopsis dialuzona*, UF 173552, 114.3 mm SL, with 2 pairs of labial barbels (usually 3 in *A. dialuzona*). Note barbels are at least twice as long as longest papilla. LB, labial barbel; MB, mandibular barbel; P, papilla; RB, rostral barbel; XB, maxillary barbel.

A sheared principal component analysis (PCA) in which the covariance matrix was factored (Humphries *et al*. 1981; Bookstein *et al*. 1985) was used to examine variation in morphometric data. The sheared second and third principal components of the data, representing shape factors independent of size, were plotted. Sheared PCA was conducted in SAS version 9.3 (SAS Institute, USA, Cary, NC).

**Molecular character and taxon sampling.** To reconstruct the evolutionary history and identify species boundaries within *Acantopsis,* a molecular phylogenetic matrix was developed consisting of one mitochondrial and one nuclear marker, *cytochrome oxidase subunit 1* (*CO1*) and *recombination-activating gene subunit 1* (*RAG1*), respectively. Tissue samples were preserved in 95% ethanol, and DNA was isolated using a DNAeasy Blood and Tissue Extraction Kit (Qiagen, inc). Primers for polymerase chain reaction (PCR) and sequencing were as follows: FISH_BCL—TCAACYAATCAYAAAGATATYGGCAC, FISH_BCH—ACTTCYGGGTGRCCRAARAATCA (Baldwin *et al.* 2009), RAG-1F—AGCTGTAGTCAGTAYCACAARATG, and RAG-RV1—TCCTGRAAGATYT TGTAGAA (Šlechtová *et al*. 2007). PCR was conducted in 25 µl reactions using the following reagents and volumes: H20 (16.75 µl), 5X Mytaq Red Buffer (4 µl) (Bioline Reagents Ltd.), primer (1 µl @ 10mM), Taq (0.25 µl @ 5U/µl), and template (1 µl). Thermocycling parameters  for PCR follow Liu *et al*. 2012. Bidirectional Sanger sequencing was performed at the University of Florida Interdisciplinary Center for Biotechnology Research. Chromatograms were trimmed, assembled, and edited using Geneious v 6.1.2 (http://www.geneious.com, Kearse 2012).

*Phylogenetic Analysis.* Consensus sequences were aligned in Mesquite v 3.11 (Maddison and Maddison, 2016) using ClustalW (Larkin *et al*. 2007). PartitionFinder v 1.1.1 (Lanfear *et al*. 2012) was used to determine the most likely partitioning scheme and models of nucleotide substitution using the models available in MrBayes and RAxML under the greedy algorithm and linked partitions. The loci were analyzed in concatenation using Maximum Likelihood (ML) and Bayesian inference (BI). The ML analyses were performed using RAxMLGUI (Silvestro and Michalak, 2012) using the ML + thorough bootstrap option with 100 runs and AutoMRE bootstrapping. BI analyses were performed using MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001; Ronquist *et al*. 2012) using the Cipres Science Gateway (Miller *et al*. 2010). MrBayes was implemented using two runs of four

chains for 24 X 10^{6} generations sampling every 1000 trees and omitting the first 8000 as burn-in. Convergence of the two runs was monitored by the average standard deviation of split frequencies, Potential Scale Reduction Factor (PSRF), and Effective Sample Sizes (ESS) of each parameter. Uncorrected p-distances were measured in MEGA v 7.0.16 (Tamura *et al*. 2007).

## Results

Characters of most taxonomic value (Table 1) include number and development of labial barbels, aspects of the color pattern, and meristic counts. In the principal component analysis of morphometric data (Table 2), size accounted for 90.1% of the observed variance (Fig. 2). The sheared second and third principal components (PC2 and PC3) accounted for 3.7% and 2.3% of the observed variance, respectively. Body depth (0.46) and caudal-peduncle length (-0.43) had the highest loadings on sheared PC2, separating the most slender species (*A. ioa*) and the most robust species (*A. thiemmedhi* and *A. dinema*) from all others. Pectoral-fin length (-0.49) had the highest loading on sheared PC3, distinguishing those with the shortest pectoral fins (*A. rungthipae* and *A. ioa*) from those with longer fins (*A. dialuzona* and *A. thiemmedhi*). Interpretation of the separation along PC3 is confounded by the fact that pectoral-fin length is known to be sexually dimorphic in adults (perhaps only during the breeding season) of at least some species, with males having longer fins. Sexes were not analyzed separately because most individuals could not be sexed reliably using only external characteristics.
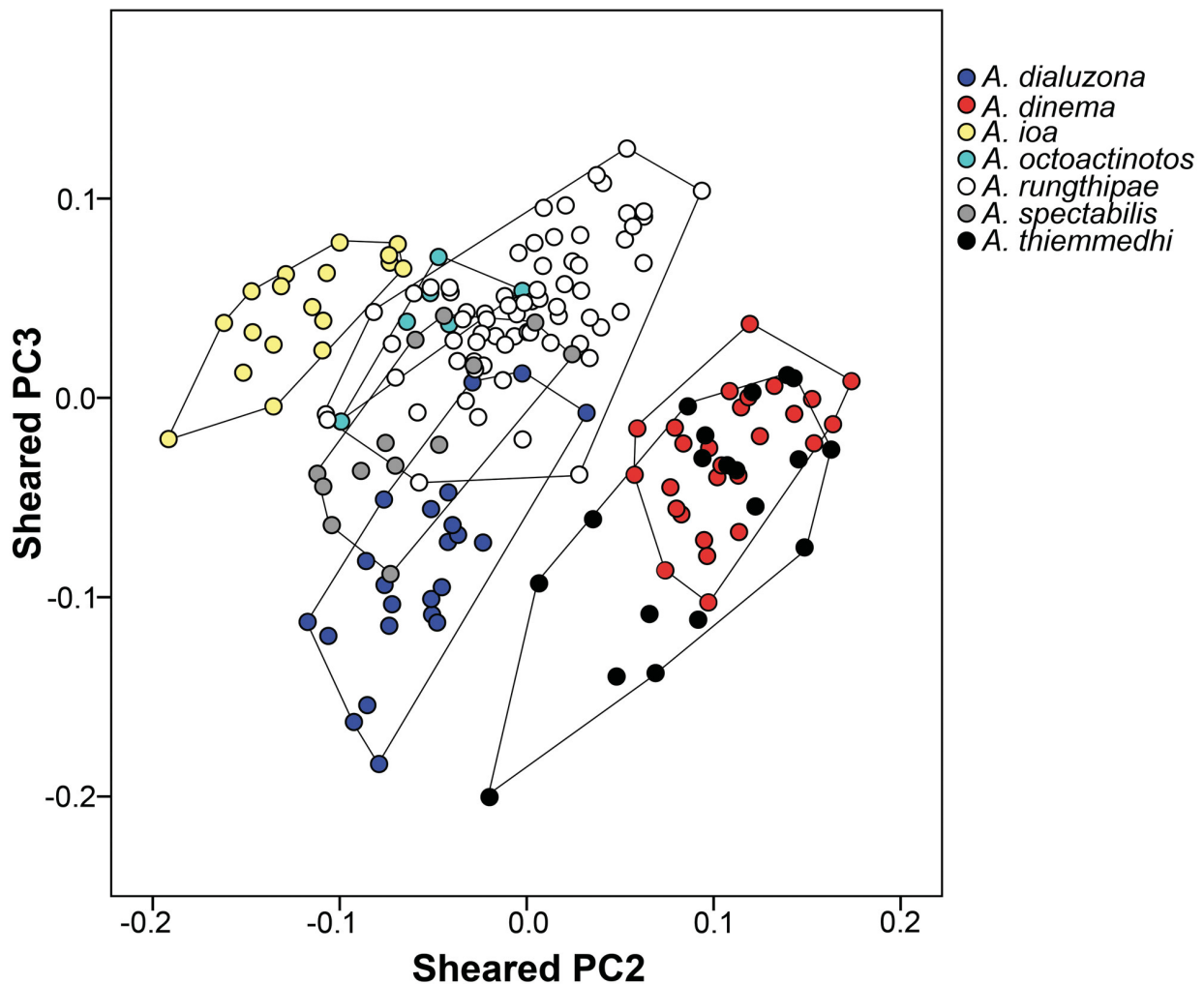


**FIGURE 2.** Principal components analysis. Size accounted for 90.1% of the observed variance. The sheared second and third principal components (PC2 and PC3) accounted for 3.7% and 2.3% of the observed variance, respectively. Body depth (0.46) and caudal-peduncle length (-0.43) had the highest loadings on sheared PC2. Pectoral-fin length (-0.49) had the highest loading on sheared PC3.

**TABLE 1.** Frequency distributions of labial barbels and meristic characteristics in species of *Acantopsis*.

| | Pairs of exposed labial barbels | | | | | | |
| | 0 | 1 | 2 | 3 | N | AVE. | S.D. |
|---|---|---|---|---|---|---|---|
| *A. dialuzona* | 1 | | 3 | 15 | 19 | 2.7 | 0.75 |
| *A. spectabilis* | | | 9 | 4 | 13 | 2.3 | 0.48 |
| *A. octoactinotos* | | | 6 | | 6 | 2.0 | 0.00 |
| *A. thiemmedhi* | | 19 | 2 | | 21 | 1.1 | 0.30 |
| *A. rungthipae* | 69 | | | | 69 | 0.0 | 0.00 |
| *A. dinema* | | | 26 | 1 | 27 | 2.0 | 0.19 |
| *A. ioa* | 18 | | | | 18 | 0.0 | 0.00 |

| | Branched dorsal-fin rays | | | | | | |
| | 8½ | 9½ | 10½ | 11½ | N | AVE. | S.D. |
|---|---|---|---|---|---|---|---|
| *A. dialuzona* | | 1 | 21 | 1 | 23 | 10.0 | 0.30 |
| *A. spectabilis* | 2 | 11 | | | 13 | 8.8 | 0.38 |
| *A. octoactinotos* | 6 | | | | 6 | 8.0 | 0.00 |
| *A. thiemmedhi* | | 1 | 19 | 1 | 21 | 10.0 | 0.32 |
| *A. rungthipae* | | 61 | 8 | | 69 | 9.1 | 0.32 |
| *A. dinema* | | | 27 | | 27 | 10.0 | 0.00 |
| *A. ioa* | | 16 | 1 | | 17 | 9.1 | 0.24 |

| | Pectoral-fin rays | | | | | |
| | 9 | 10 | 11 | N | AVE. | S.D. |
|---|---|---|---|---|---|---|
| *A. dialuzona* | 1 | 19 | 3 | 23 | 10.1 | 0.42 |
| *A. spectabilis* | | 11 | 2 | 13 | 10.2 | 0.38 |
| *A. octoactinotos* | 4 | 2 | | 6 | 9.3 | 0.52 |
| *A. thiemmedhi* | 3 | 13 | 5 | 21 | 10.1 | 0.62 |
| *A. rungthipae* | 4 | 54 | 11 | 69 | 10.1 | 0.46 |
| *A. dinema* | 7 | 19 | 1 | 27 | 9.8 | 0.51 |
| *A. ioa* | 1 | 15 | 2 | 18 | 10.1 | 0.42 |

| | Midlateral spots | | | | | | | |
| | 6–9 | 10–13 | 14–17 | 18–21 | N | AVE. | RANGE | S.D. |
|---|---|---|---|---|---|---|---|---|
| *A. dialuzona* | 8 | 15 | | | 23 | 10.0 | 7–13 | 1.55 |
| *A. spectabilis* | 1 | 11 | 1 | | 13 | 11.5 | 9–15 | 1.66 |
| *A. octoactinotos* | 1 | 5 | | | 6 | 10.8 | 8–13 | 1.83 |
| *A. thiemmedhi* | 20 | 1 | | | 21 | 7.5 | 6–10 | 1.03 |
| *A. rungthipae* | 7 | 40 | 8 | | 55 | 11.7 | 9–17 | 1.83 |
| *A. dinema* | 7 | 7 | | | 14 | 9.1 | 6–12 | 2.16 |
| *A. ioa* | | 1 | 10 | 7 | 18 | 16.8 | 13–21 | 2.43 |

| Dorsal saddles | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | 5–10 | 11–17 | 18–23 | N | AVE. | RANGE | S.D. |
| *A. dialuzona* | | 23 | | 23 | 13.3 | 11–17 | 1.60 |
| *A. spectabilis* | 3 | 10 | | 13 | 10.9 | 9–12 | 1.04 |
| *A. octoactinotos* | | 6 | | 6 | 14.1 | 11–17 | 2.01 |
| *A. thiemmedhi* | 21 | | | 21 | 8.3 | 7–9 | 0.66 |
| *A. rungthipae* | 2 | 47 | 3 | 52 | 13.8 | 10–20 | 2.01 |
| *A. dinema* | 1 | 19 | | 20 | 13.6 | 8–17 | 2.19 |
| *A. ioa* | | 4 | 14 | 18 | 19.4 | 15–23 | 2.43 |

| Abdominal vertebrae | | | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | N |
| *A. dialuzona* | | 1 | 1 | 5 | | | | | 7 |
| *A. spectabilis* | | | | 1 | 2 | | | | 3 |
| *A. octoactinotos* | 2 | 1 | | | | | | | 3 |
| *A. thiemmedhi* | 1 | | 2 | | | | | | 3 |
| *A. rungthipae* | | 1 | 6 | 8 | | | | | 15 |
| *A. dinema* | | 1 | 1 | 3 | | | | | 5 |
| *A. ioa* | | | | | | 1 | 2 | 2 | 5 |

| Caudal vertebrae | | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | 10 | 11 | 12 | 13 | 14 | N |
| *A. dialuzona* | | 3 | 3 | 1 | | 7 |
| *A. spectabilis* | | | 3 | | | 3 |
| *A. octoactinotos* | | | 1 | 2 | | 3 |
| *A. thiemmedhi* | 1 | 2 | | | | 3 |
| *A. rungthipae* | | 7 | 8 | | | 15 |
| *A. dinema* | 1 | 3 | | 1 | | 5 |
| *A. ioa* | | | | 4 | 1 | 5 |

| Total vertebrae | | | | | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | N |
| *A. dialuzona* | | | | 5 | 2 | | | | | | 7 |
| *A. spectabilis* | | | | 1 | 2 | | | | | | 3 |
| *A. octoactinotos* | | | 2 | 1 | | | | | | | 3 |
| *A. thiemmedhi* | 1 | 1 | 1 | | | | | | | | 3 |
| *A. rungthipae* | | | 4 | 7 | 4 | | | | | | 15 |
| *A. dinema* | | | 2 | 3 | | | | | | | 5 |
| *A. ioa* | | | | | | | | 1 | 1 | 3 | 5 |

**TABLE 2.** Morphometric data for recognized species of *Acantopsis*.

| | *A. dialuzona* N=23 | | | *A. spectabilis* N=13 | | | *A. octoactinotos* N=6 | | | *A. thiemmedhi* N=19 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | AVE. | RANGE | S.D. | AVE. | RANGE | S.D. | AVE. | RANGE | S.D. | AVE. | RANGE | S.D. |
| Standard length (mm) | | 55.2–138.6 | | | 53.8–162.9 | | | 71.6–85.6 | | | 80.2–153.3 | |
| **% STANDARD LENGTH** | | | | | | | | | | | | |
| Total length | 120.9 | 117.6–123.2 | 1.29 | 119.2 | 116.9–123.4 | 2.05 | 117.2 | 116.3–118.0 | 0.63 | 122.1 | 118.9–124.9 | 1.26 |
| Body depth | 10.0 | 8.9–11.9 | 0.84 | 10.1 | 9.0–11.6 | 0.76 | 10.5 | 9.6–11.2 | 0.50 | 13.1 | 9.8–16.6 | 1.71 |
| Body width | 7.9 | 6.4–9.1 | 0.70 | 7.9 | 6.8–9.4 | 0.77 | 7.5 | 6.8–7.9 | 0.37 | 8.8 | 5.8–10.3 | 1.17 |
| Predorsal length | 50.4 | 48.1–53.5 | 1.38 | 51.0 | 49.2–54.3 | 1.58 | 50.7 | 50.1–52.0 | 0.82 | 51.1 | 49.2–54.2 | 1.16 |
| Prepectoral length | 25.0 | 22.6–27.7 | 1.44 | 22.7 | 21.0–24.4 | 1.07 | 23.2 | 22.4–24.6 | 0.84 | 24.2 | 22.0–26.5 | 1.14 |
| Prepelvic length | 55.0 | 52.7–58.3 | 1.47 | 54.1 | 52.7–56.1 | 1.05 | 53.0 | 52.1–53.5 | 0.55 | 55.6 | 53.3–56.8 | 0.87 |
| Preanal length | 79.8 | 77.6–81.7 | 1.18 | 79.1 | 77.5–81.3 | 1.13 | 77.0 | 75.6–77.8 | 0.77 | 79.8 | 78.0–81.5 | 1.04 |
| Caudal-peduncle length | 14.6 | 12.5–16.2 | 0.81 | 14.6 | 12.9–16.6 | 1.17 | 16.6 | 16.1–17.2 | 0.48 | 13.6 | 12.5–14.7 | 0.66 |
| Caudal-peduncle depth | 4.6 | 4.0–4.9 | 0.21 | 4.5 | 4.1–5.1 | 0.31 | 4.7 | 4.3–5.2 | 0.28 | 5.7 | 5.0–6.3 | 0.38 |
| Dorsal-fin base length | 13.6 | 12.9–14.6 | 0.42 | 12.1 | 11.0–13.0 | 0.52 | 11.8 | 11.2–12.6 | 0.51 | 14.4 | 12.1–15.8 | 0.86 |
| Anal-fin base length | 6.9 | 6.1–7.7 | 0.41 | 7.0 | 6.3–7.6 | 0.40 | 7.5 | 7.2–7.7 | 0.20 | 7.6 | 6.9–8.4 | 0.44 |
| Dorsal-fin length | 19.2 | 18.0–20.3 | 0.59 | 17.6 | 16.2–18.7 | 0.68 | 18.1 | 17.4–19.1 | 0.60 | 21.6 | 18.7–23.0 | 1.04 |
| Pectoral-fin length | 17.0 | 14.7–18.9 | 0.97 | 15.8 | 14.2–17.6 | 0.95 | 14.8 | 14.5–15.1 | 0.22 | 18.7 | 16.1–22.0 | 1.79 |
| Pelvic-fin length | 12.1 | 11.1–13.2 | 0.51 | 11.5 | 10.5–12.5 | 0.52 | 12.2 | 11.9–12.7 | 0.32 | 13.6 | 12.6–14.5 | 0.53 |
| Anal-fin length | 12.3 | 11.2–13.4 | 0.54 | 12.0 | 11.6–12.5 | 0.33 | 13.2 | 12.7–13.5 | 0.32 | 14.1 | 13.1–15.0 | 0.52 |
| Head length | 26.1 | 22.9–29.7 | 1.64 | 23.3 | 21.8–25.7 | 1.18 | 23.3 | 22.5–24.6 | 0.81 | 24.8 | 22.6–26.8 | 1.24 |
| **% HEAD LENGTH** | | | | | | | | | | | | |
| Head depth | 40.3 | 37.6–46.0 | 2.20 | 41.8 | 39.6–44.8 | 1.71 | 42.8 | 40.0–44.4 | 1.56 | 47.6 | 44.3–52.8 | 2.27 |
| Snout length | 65.5 | 59.5–71.8 | 3.76 | 66.1 | 60.1–70.3 | 3.35 | 55.5 | 53.7–58.4 | 1.76 | 62.5 | 57.5–68.3 | 2.83 |
| Postorbital-head length | 30.3 | 27.2–32.4 | 1.55 | 31.3 | 28.4–34.3 | 1.67 | 37.6 | 35.2–39.8 | 1.78 | 32.7 | 30.0–34.9 | 1.46 |
| Eye length | 14.0 | 11.0–15.6 | 1.33 | 13.7 | 11.5–17.2 | 1.90 | 13.9 | 12.7–15.3 | 0.93 | 14.6 | 13.0–16.4 | 0.92 |

**TABLE 2.** (Continued). Data for holotype (abbr. holo.) included in average and standard deviation for each species.

| | A. rungthipae N=69 | | | | A. dinema N=27 | | | | A. ioa N=18 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | HOLO. | AVE. | RANGE | S.D. | HOLO. | AVE. | RANGE | S.D. | HOLO. | AVE. | RANGE | S.D. |
| Standard length (mm) | 107.4 | | 51.3–132.4 | | 100.7 | | 81.3–116.7 | | 128.4 | | 82.9–132.0 | |
| % STANDARD LENGTH | | | | | | | | | | | | |
| Total length | 118.2 | 119.0 | 116.0–121.3 | 1.02 | 121.2 | 120.85 | 119.0–123.3 | 1.02 | 114.1 | 115.8 | 114.1–117.4 | 0.83 |
| Body depth | 11.1 | 11.2 | 9.0–14.2 | 0.83 | 12.0 | 13.18 | 12.0–14.5 | 0.66 | 9.4 | 9.7 | 8.5–11.0 | 0.75 |
| Body width | 8.1 | 8.2 | 5.3–10.3 | 0.80 | 8.8 | 9.05 | 8.0–10.3 | 0.75 | 6.2 | 6.9 | 5.2–7.9 | 0.66 |
| Predorsal length | 49.3 | 50.0 | 47.4–53.6 | 1.10 | 48.0 | 49.76 | 48.0–51.4 | 0.84 | 51.2 | 52.3 | 50.6–53.8 | 1.11 |
| Prepectoral length | 22.2 | 22.5 | 20.8–24.4 | 0.91 | 23.2 | 24.56 | 23.2–25.8 | 0.67 | 22.0 | 22.3 | 21.3–23.9 | 0.60 |
| Prepelvic length | 53.9 | 54.5 | 44.3–58.4 | 1.57 | 54.8 | 55.04 | 53.4–56.8 | 0.97 | 55.2 | 55.8 | 54.3–58.3 | 1.08 |
| Preanal length | 80.5 | 79.3 | 69.3–82.5 | 1.51 | 80.0 | 80.64 | 79.4–82.1 | 0.60 | 77.6 | 78.8 | 77.0–80.2 | 0.86 |
| Caudal-peduncle length | 13.4 | 14.4 | 11.5–16.1 | 0.82 | 13.8 | 13.13 | 12.1–14.3 | 0.56 | 15.8 | 14.7 | 13.1–16.2 | 0.84 |
| Caudal-peduncle depth | 5.0 | 5.2 | 4.7–6.1 | 0.30 | 5.6 | 5.67 | 5.3–6.2 | 0.23 | 4.5 | 4.7 | 4.2–5.1 | 0.23 |
| Dorsal-fin base length | 12.8 | 13.1 | 11.4–14.6 | 0.60 | 15.2 | 15.05 | 14.0–16.0 | 0.52 | 12.2 | 11.7 | 10.9–13.1 | 0.63 |
| Anal-fin base length | 7.0 | 7.0 | 6.0–8.0 | 0.40 | 7.6 | 7.04 | 5.8–7.8 | 0.44 | 7.2 | 7.3 | 6.2–8.8 | 0.60 |
| Dorsal-fin length | 18.2 | 18.4 | 17.1–20.2 | 0.68 | 21.6 | 21.09 | 20.0–22.0 | 0.49 | 15.5 | 15.7 | 13.6–17.0 | 0.77 |
| Pectoral-fin length | 14.7 | 14.7 | 13.1–22.5 | 1.19 | 16.1 | 17.50 | 14.9–21.3 | 1.69 | 12.5 | 13.6 | 12.3–14.9 | 0.82 |
| Pelvic-fin length | 10.7 | 11.0 | 9.9–12.0 | 0.44 | 13.3 | 12.92 | 12.1–13.6 | 0.37 | 10.0 | 10.2 | 9.6–10.6 | 0.30 |
| Anal-fin length | 11.5 | 11.9 | 11.0–12.8 | 0.48 | 13.7 | 13.39 | 12.5–14.2 | 0.38 | 11.0 | 11.3 | 10.5–13.0 | 0.58 |
| Head length | 22.5 | 23.3 | 21.6–25.6 | 0.98 | 24.3 | 25.26 | 24.1–26.9 | 0.65 | 22.5 | 23.1 | 21.8–24.2 | 0.68 |
| % HEAD LENGTH | | | | | | | | | | | | |
| Head depth | 43.8 | 43.1 | 38.3–46.9 | 1.85 | 45.7 | 46.21 | 43.9–48.7 | 1.40 | 40.8 | 39.9 | 38.0–41.2 | 0.88 |
| Snout length | 63.6 | 62.1 | 54.7–68.7 | 2.66 | 60.4 | 61.08 | 58.8–65.9 | 1.65 | 66.8 | 64.2 | 61.0–69.6 | 2.01 |
| Postorbital-head length | 31.8 | 33.4 | 30.2–37.8 | 1.63 | 35.1 | 34.78 | 32.9–38.6 | 1.28 | 31.8 | 31.9 | 30.4–34.3 | 1.07 |
| Eye length | 13.6 | 13.6 | 11.5–16.4 | 1.05 | 13.5 | 13.62 | 11.5–15.6 | 1.04 | 12.5 | 13.0 | 11.8–15.1 | 0.90 |

Among the most emblematic attributes of *Acantopsis* are the long head and long snout. However, the taxonomic value of these characters at the species level is reduced by the fact that their relative proportions change with growth. In particular, the relative snout length increases with standard length (Fig. 3). Although the snout length/HL for a syntype of *Acantopsis dialuzona* (RMNH 2707) is proportionally 8.3% shorter (64.7%) than that of the lectotype (RMNH 4977) of *Cobitis choirorhynchos* (73.0%), both specimens are within variation typical for *A. dialuzona* (Fig. 3A). The head length did not increase disproportionately to standard length.
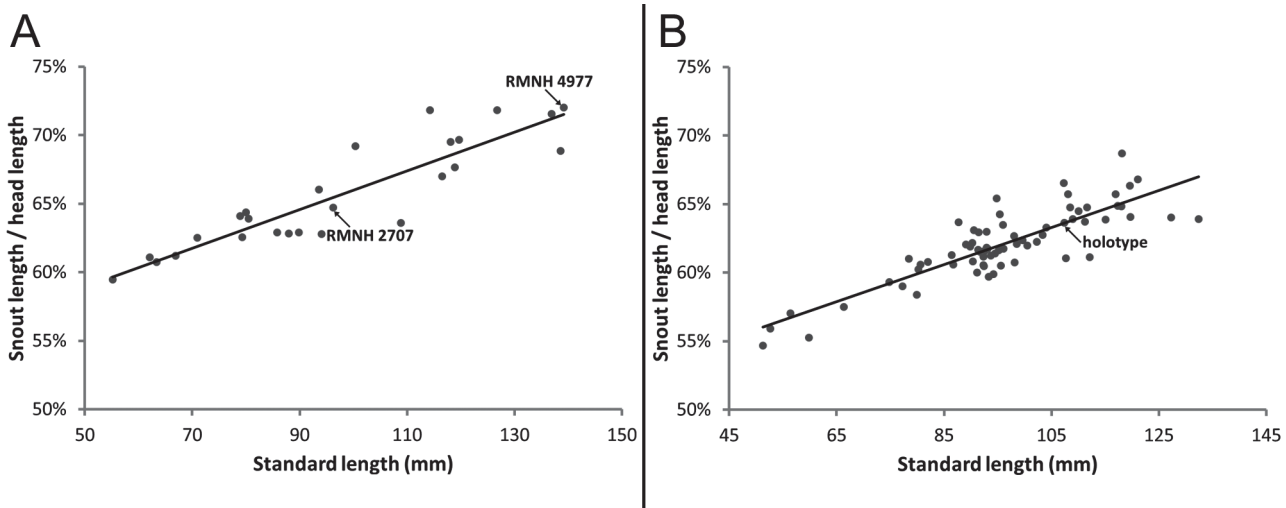


**FIGURE 3**. Snout length/head length relative to standard length in (A) *Acantopsis dialuzona* (Y = 0.141X + 51.887; $r^2$ = 0.813), and (B) *A. rungthipae* (Y = 0.136X + 49.056, $r^2$ = 0.722). Dots represent specimens measured. RMNH 2707 is the value for the syntype of *Acantopsis dialuzona*, and RMNH 4977 is the value for the lectotype of *Cobitis choirorhynchos.*

The two-gene molecular dataset consisted of 111 *Acantopsis* individuals collected from 40 localities across much of Southeast Asia (Appendix B). Three representatives of the superfamily Cobitoidea were downloaded from GenBank and included as outgroup taxa: *Aperioptus gracilentus* (*CO1*-AP013298 and *RAG1*-EF508600), *Kottelatlimia pristes* (*CO1*-AP011343 and *RAG1*-EF508639), and *Balitoropsis zollingeri* (*CO1*-KR052865 and *RAG1*-KP322535) (Šlechtová *et al*. 2008, Randall and Riggs 2015, Randall and Page 2015). All terminal taxa were represented by both *CO1* (avg. 644 nt) and *RAG1* (avg. 846 nt). Alignments of neither locus contained insertions, deletions, nor stop codons. The following partitioning schemes and models of nucleotide substitution were implemented: BI- *CO1*_1=SYM+I, *CO1*_2=HKY, *CO1*_3=GTR+I+G, *RAG1*_1 and *RAG1*_2=K80+I, *RAG1*_3=GTR+G; ML- *CO1*_1 and *RAG1*_1=GTR+G, *CO1*_2 and *RAG1*_2=GTR+G, *CO1*_3=GTR+G, *RAG1*_+3=GTR+G. Convergence of the BI runs was supported by the average standard deviation of split frequencies (0.008), average PSRF values (1.000), and high ESS values (min=2257.36, avg=11431.05). Mean interspecific and intraspecific *CO1* p-distances ranged from 12.10% to 15.39% and 0.05% to 4.40%, respectively, and mean interspecific and intraspecific *RAG1* p-distances ranged from to 0.85% to 3.12% and 0.00% to 0.54%, respectively (Table 3).

**TABLE 3.** Mean within-group p-distances (on diagonal; *RAG1/CO1*) and mean between-group p-distances (upper triangle—*RAG1*; lower triangle—*CO1*).

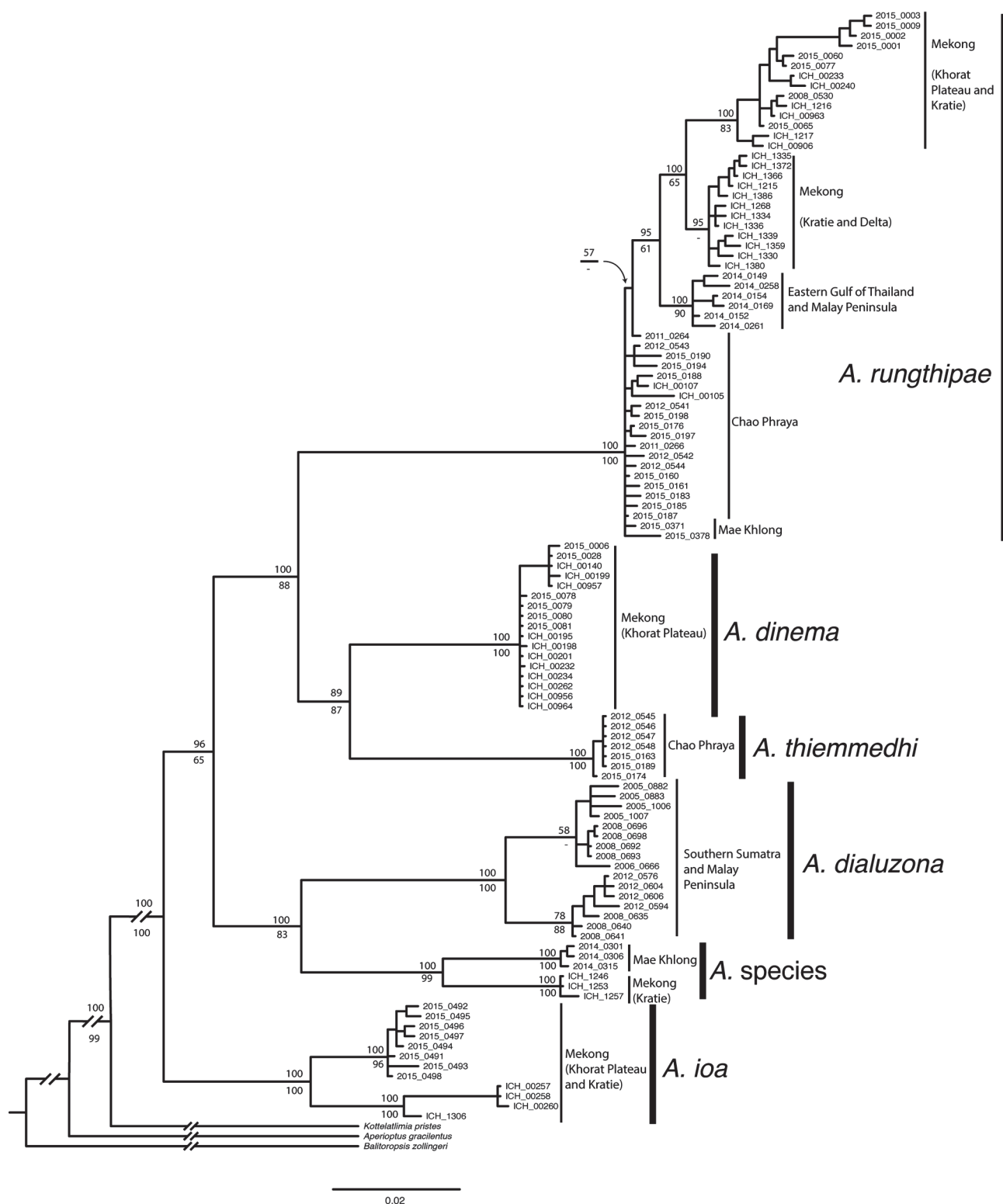|  | A. rungthipae | A. dinema | A. thiemmedhi | A. dialuzona | A. species | A. ioa |
|---|---|---|---|---|---|---|
| *A. rungthipae* | 0.11%/2.45% | 2.39% | 3.12% | 2.23% | 2.51% | 2.64% |
| *A. dinema* | 12.10% | 0.05%/0.57% | 1.63% | 1.24% | 1.76% | 1.89% |
| *A. thiemmedhi* | 12.34% | 12.56% | 0.0%/0.05% | 1.52% | 2.04% | 2.10% |
| *A. choirorhynchos* | 14.67% | 14.06% | 14.33% | 0.31%/2.25% | 0.85% | 0.99% |
| *A. species* | 14.82% | 14.16% | 15.18% | 13.39% | 0.54%/4.40% | 1.26% |
| *A. ioa* | 13.61% | 12.87% | 13.87% | 14.99% | 15.39% | 0.49%/3.61% |

**FIGURE 4.** Combined (*CO1+RAG1*) Bayesian phylogenetic reconstruction of *Acantopsis*. BI posterior probabilities and ML bootstrap support are plotted above and below branch lengths, respectively. The geographic distribution of each major clade is described using the freshwater ecoregions delimited by Abell *et al.* (2008).

The BI reconstruction is shown in Figure 4 along with the ML bootstrap values. To facilitate legibility of Figure 4, support values were omitted for clades that are not relevant to the discussion. *Acantopsis* is strongly supported as monophyletic and sister to *Kottelatlimia pristes*. Six species-level clades within *Acantopsis* are resolved and well supported, four of which are previously unrecognized species, and three of which are described herein. Within *Acantopsis, A. rungthipae* n. sp. is sister to a clade containing *A. dinema* n. sp. and *A. thiemmedhi*.

*Acantopsis dialuzona* is sister to an undescribed species containing specimens from the Mae Khlong and Mekong (Kratie-Stung Treng Ecoregion). These two clades are sister to one another, and *A. ioa* n. sp. is the sister to all other species of *Acantopsis* included in the analysis. No genetic material from specimens of *A. spectabilis* or *A. octoactinotos* was available.

### *Acantopsis* van Hasselt 1823

*Acantopsis* van Hasselt, 1823: 133 (type species: *Acantopsis dialuzona* van Hasselt, 1823: 133, by monotypy)
*Acanthopsis* van Hasselt, 1824: 376, 377 (incorrect spelling of *Acantopsis*)
*Prostheacanthus* Blyth, 1860: 167 (type species: *Prostheacanthus spectabilis* Blyth, 1860: 167, by monotypy)

*Acantopsis* and the type species, *Acantopsis dialuzona*, were described in a letter from J. C. van Hasselt to C. J. Temminck, director of the Leiden Museum. Temminck published the letter in 1823, making van Hasselt's name available (Kottelat 1987). Alfred (1961b) provided an English translation of the original description:
  "*Acantopsis* distinguishes itself from them [referring to *Acantophthalmus*, a synonym of *Cobitis*] by a very elongate pointed face which in those is blunt and so short that the eyes are situated nearly in a vertical line with the mouth-opening. Owing to this elongation the moveable spines are situated far in front of the eyes and the whole form too divergent (for them) to be combined with each other. I found this animal in the river at Batavia and in my drawing it bears the name Dialuzona Mihi."
  Roberts (1993) provided a previously unpublished but more informative description and a watercolor of *A. dialuzona* by Valenciennes (fig. 25), a drawing by J. Werner based on RMNH 2707—the type of *A. dialuzona* (fig. 59), and a vertebral count of 30 abdominal +14 caudal = 44 for the type. The description and illustrations were apparently intended for, but were not included in, the *Histoire naturelle des Poissons* (Cuvier and Valenciennes 1846). The description included: "Compressed body and head, more pointed snout than in *Cobitis*. Eyes on top of head, almost touching, preceded by pointed spines. Very small mouth, very short barbels. Dorsal fin in middle of body. Long, pointed pectoral fin. Reddish back, white belly, silvery stripe along side of body, 8–9 darker gray oblong spots. Greenish-gray caudal fin with black dot at upper base. Dorsal-fin rays 11; pectoral-fin rays 10; pelvic-fin rays 7, anal-fin rays 6, caudal-fin rays 15."
  Bleeker (1860) redescribed *A. dialuzona* based on additional specimens collected from Batavia [Jakarta]. The description was reproduced in English in van Oijen and Loots (2012:76–77, fig. 4), along with an illustration from the *Atlas Ichthyologique* (Bleeker 1863–1864) of the original drawing of the type left in Java by van Hasselt, as noted by Roberts (1993).
  **Diagnosis.** Cobitidae. Distinguished from all other genera by the erectile, bifid 'suborbital' spine being far forward, approximately midway between the eye and the tip of the long snout (Fig. 5). In other genera of cobitids, the spine is located under or slightly anterior to the eye, never midway between the eye and the tip of the snout.
  The only other cobitid genus in mainland Southeast Asia with a similar body shape and color pattern is *Aperioptus* Richardson (Siebert 1991a, Page and Tangjitjaroen 2015), which is distinguished from *Acantopsis* by having the suborbital spine only slightly anterior to the eye (reaching posteriorly to at least the anterior margin of the eye), 7 branched dorsal-fin rays (8 or more in *Acantopsis*), and the dorsal-fin origin over, slightly anterior, or slightly posterior to the pelvic-fin origin (vs. far in front of the pelvic-fin origin in *Acantopsis*). Although morphologically similar, molecular data indicate that *Kottelatlimia* may be more closely related to one of these two genera than *Acantopsis* and *Aperioptus* are to each other (Fig. 4, Šlechtová *et al.* 2008, Havird *et al.* 2010).
  **Description.** Body long and slender, deepest predorsally; straight to slightly arched predorsally, tapering from origin of dorsal fin to narrow caudal peduncle. Venter flat, tapering from origin of pelvic fins, more strongly from origin of anal fin, to caudal peduncle. Dorsal-fin origin far in front of pelvic-fin origin. Head long (22–30% SL); snout long (54–72% HL), pointed, steeply sloped to nape. Suborbital spine bifid, medial point longest (Fig. 5), located near midpoint between eye and tip of snout. Groove containing spine ending below anterior margin of eye; spine ending well before eye. Eye round, subcutaenous, high on rear half of head; interorbital distance less than eye diameter. Window to gas bladder posterior to dorsal limb of cleithrum. Scales absent on head and breast, usually absent along midline of abdomen; rest of body covered with ctenoid scales; scales typically embedded on nape, lower side of body, and often anteriorly on side of body. Caudal fin forked in large individual, emarginated in small individual; lobes subequal. Lateral line complete, extending onto caudal fin for short distance. Branched dorsal

rays 8½–11½; branched caudal rays 14, 7 in upper, 7 in lower lobe; branched anal rays 5½; pectoral rays 9–11; pelvic rays 7; 28–35 abdominal plus 10–14 caudal = 39–48 total vertebrae. One pair each of rostral, maxillary, and mandibular barbels; 0–3 pairs of labial barbels. Maximum SL = 212.5 mm, TL = 242.5 mm (*A. spectabilis*, NIFI 2456).

**Color.** Color patterns vary inter- and intraspecifically. Variation within species, and possibly among species, appears to be related to habitat with darker patterns on individuals living on mixed sand and gravel or in clear water, and lighter patterns on those living on sand only or in turbid water. Intraspecific variation in color can be extreme and is probably in large part accountable for the taxonomic confusion that has surrounded this genus.
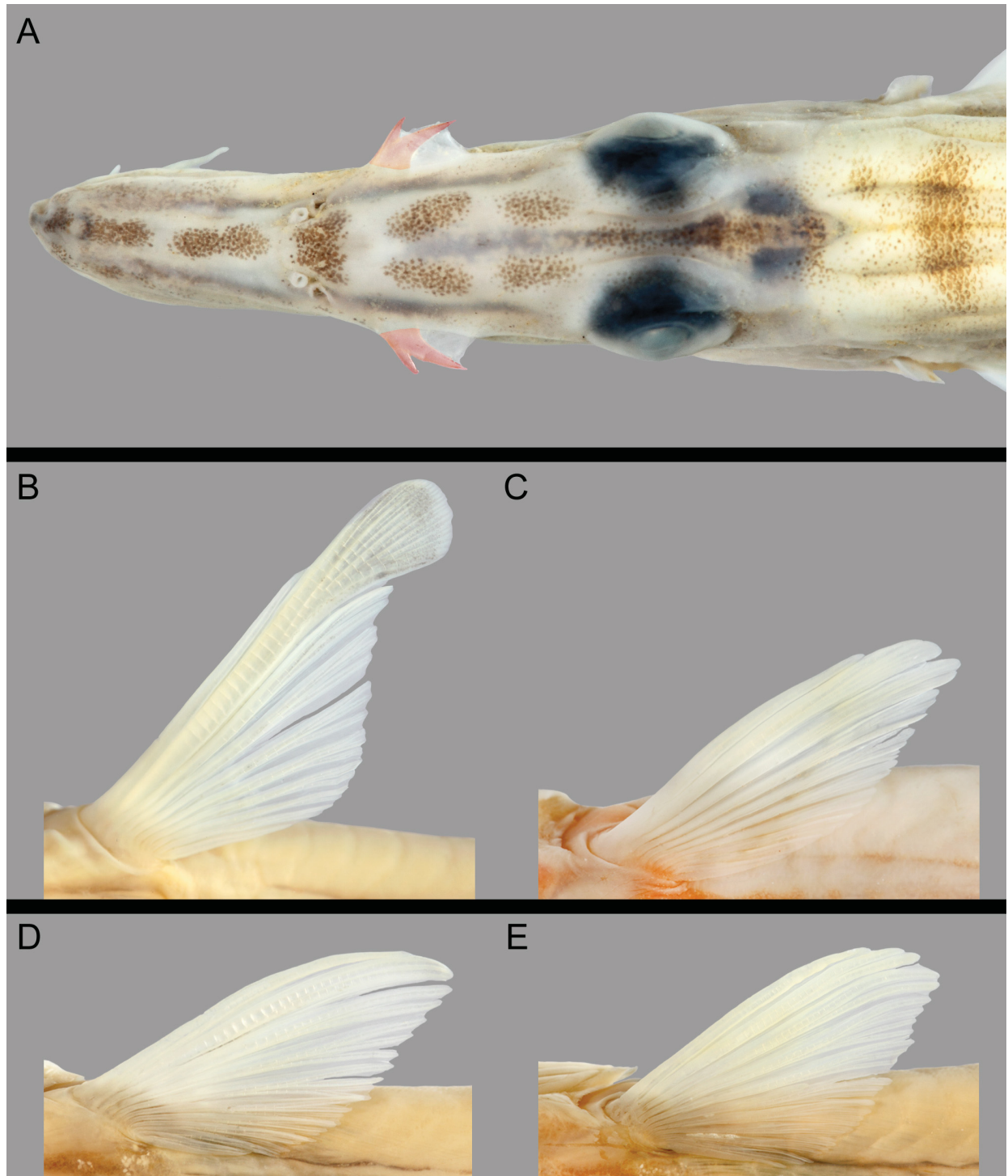


**FIGURE 5**. (A) Dorsal view of erectile, bifid 'suborbital' spine (highlighted) on snout of *A. rungthipae*, UF 188112, 70.0 mm SL. Pectoral fins of *A. dinema*, (B) UF 185131, 90.3 mm SL male, and (C) UF 188116, paratype, 108.9 mm SL female; and *A. rungthipae* (D) UF 235976, paratype, 94.5 mm SL male, and (E) THNHM F0013610, holotype, 107.4 mm SL female.

The most conspicuous aspects of the color pattern of all species are the 1–2 rows of dark-brown to black spots on top of the head, continuing as a row of saddles along the dorsal midline to the origin of the caudal fin, and a row of smaller dark spots or blotches along the midside of the body from the head to the origin of the caudal fin. Spots on top of the head are in one row anterior to the nares and one or two rows posterior to the nares. Dorsal saddles and spots along the side may be faint, and the latter are often obscured by a dusky to dark line along the lateral line. Less well-defined dark spots, blotches, and reticulations may occur on the upper side, and less often on the lower side. Other dark brown to black pigment may include spots on the cheek and opercle, sometimes as 1–2 well-defined rows of large spots with many smaller spots above; large spots or dusky bands on the dorsal, caudal, anal, and paired fins; and a small black spot near the upper margin of the origin of the caudal fin, sometimes developed as an ocellus. The lower side of the head, breast, and belly are white.

In life, large individuals have a faint yellow to reddish brown cast dorsally, are translucent white ventrally, and have a green iridescence on the side of the head. Fins are mostly clear but with dusky bands on some or all fins, black spots in the dorsal and caudal fins, and a faint yellowish cast on the paired and anal fins (Inger and Chin 1962, pers. obs.). Some species have a reddish-brown streak along the lower caudal-fin margin near the base. Smaller individuals are more translucent and have less contrasting color patterns.

**Sexual dimorphism.** Males have a longer, ramified first branched pectoral-fin ray as noted by Inger and Chin (1962) and Siebert (1991b, fig. 3), and a distal lobe on the first branched pectoral-fin ray in at least one species (*A. dinema*, Fig. 5). In some, perhaps all species males reach a smaller adult size. In the largest series of specimens examined, (UF 188116; *A. dinema*) males (N = 15) averaged 88.1 mm SL, and females (N = 45) averaged 99.5 mm SL. In at least some species, the medial point of the suborbital spine is longer and more curved in males (Siebert 1991b). Interspecific and seasonal variation in sexually dimorphic characteristics, perhaps including color, remains mostly unknown in *Acantopsis*.

## *Acantopsis dialuzona* van Hasselt, 1823
Piglet Horseface Loach
(Fig. 6)

*Acantopsis Dialuzona* van Hasselt, 1823: 133 (type locality: Indonesia: Java: Batavia [present-day Jakarta]; syntypes: RMNH 2707 [1]; unpublished van Hasselt's figure reproduced in Roberts, 1993: fig. 25)
*Acanthopsis biaculeata* Rüppell, 1852:28 (nomen nudum, Kottelat 2012)
*Cobitis choirorhynchos* Bleeker, 1854:95. (type locality: Indonesia: Sumatra: Palembang: at confluence of Lematang and Enim Rivers; lectotype: RMNH 4977, designated by Alfred 1961a:33)
*Cobitis macrorhynchos* Bleeker, 1854:95 (unnecessary replacement name for *Acantopsis dialuzona* van Hasselt, 1823: 133)

**Diagnosis.** *Acantopsis dialuzona* differs from all other species of *Acantopsis* (Table 4) by combination of usually 3 pairs of labial barbels, well developed ocellus on upper margin of caudal-fin base, 0–1 row of large spots on side of head, no large black spots on dorsal or caudal fins, rarely black specks beneath midlateral row of black spots, usually 10½ branched dorsal rays and 10 pectoral rays, 11–17 dark saddles along dorsal midline, 7–13 black spots along side of body, 42–43 total vertebrae, body depth 8.9–11.9% SL, body width 6.4–9.1% SL, caudal-peduncle length 12.5–16.2% SL.

**Comparisons.** *Acantopsis dialuzona* is distinguished from all species of *Acantopsis* by having a well developed ocellus on the upper margin of the caudal-fin base, and from all species except *A. spectabilis* by having 3 (vs. 0–2) pairs of labial barbels. *Acantopsis dialuzona* differs from *A. spectabilis* and *A. thiemmedhi* in lacking conspicuous black spots, blotches, or bands on the caudal, anal, and paired fins, and from *A. thiemmedhi* in lacking a large black blotch on the tip of the anterior rays of the dorsal fin. It further differs from *A. dinema* in having large black spots on side of head, a less deep body (8.9–11.9 vs. 12.0–14.5), and lacking many black specks beneath midlateral row of black spots. It further differs from *A. spectabilis, A. rungthipae,* and *A. ioa* by having usually 10½ (vs. 9½) branched dorsal rays, from *A. ioa* by having 42–43 (vs. 46–48) total vertebrae, and from *A. octoactinotos* by having usually 10½ (vs. 8½) branched dorsal rays, usually 10 (vs. 9) pectoral rays, large dark spots on side of head.

**Description.** As in description of genus; Tables 1, 2, 4. Head long (22.9–29.7% SL); snout long (59.5–71.8% HL); 3, rarely 0–2, pairs of labial barbels; 10½, rarely 9½ or 11½, branched dorsal rays; 10, rarely 9 or 11, pectoral

rays; 28–31 abdominal + 11–14 caudal = 42–44 total vertebrae (Table 1; Roberts 1989, 1993). Maximum SL = 183.6 mm, TL = 221.8 mm (UF 235414).

**Color.** Dark spots in 1 or 2 rows on top of head, scattered or in 1 poorly defined row on side of head. Eleven–17 dark saddles along dorsal midline; 7–13 large dark spots or blotches along lateral line from head to caudal fin; dark spots or reticulations on upper side of body. Dark pigment on lower side highly variable; usually absent, but rarely with many dark specks. Four–5 faint bands on dorsal and caudal fins; other fins with no or faint bands; caudal fin sometimes with dark lower margin. Bold black spot in center of ocellus near upper margin of caudal-fin origin.
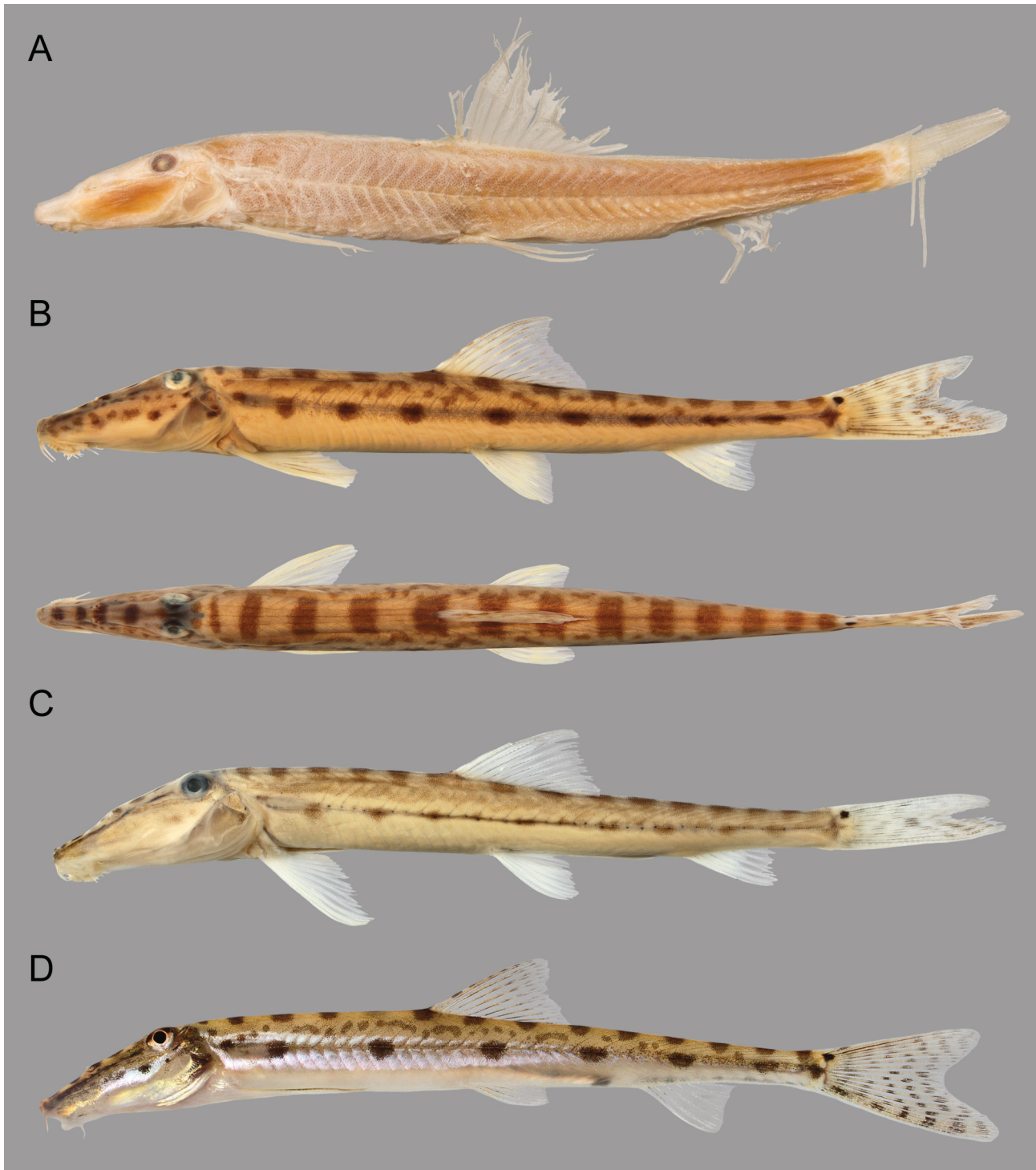


**FIGURE 6**. *Acantopsis dialuzona*. (A) Lateral view, syntype, RMNH 2707, 96.2 mm SL. (B) Lateral and dorsal views, UF 235416, 120.5 mm SL. (C) Lateral view, UF 166886, 93.6 mm SL. (D) Live view, UF 236150, 73.7 mm SL.
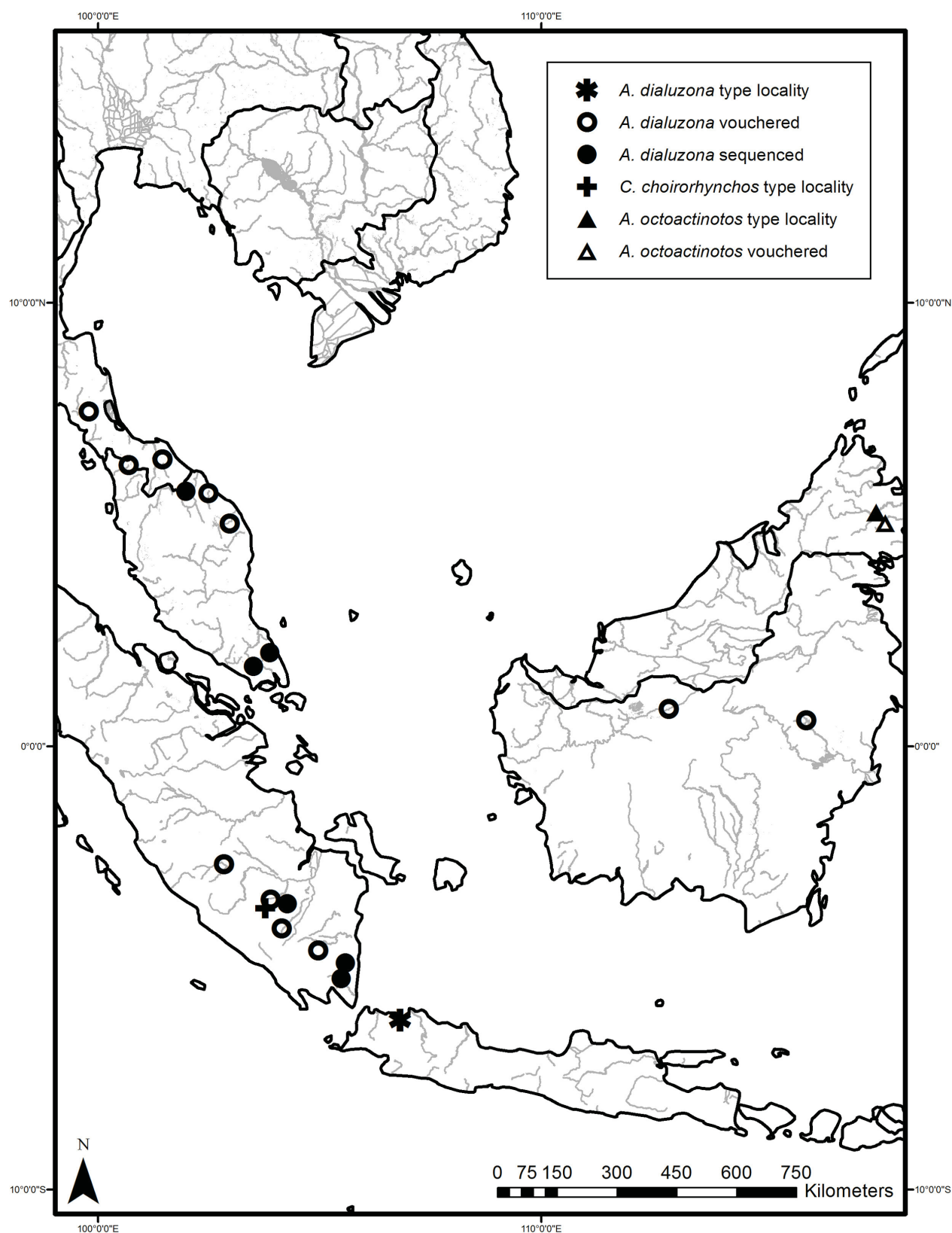
**FIGURE 7.** Localities of specimens examined of *Acantopsis dialuzona*, including type locality of *Cobitis choirorhynchos*, and *A. octoactinotos*.

**TABLE 4.** Diagnostic features of species of *Acantopsis*. *Data from Siebert (1991b), Sontirat (1999), or Vishwanath and Laisram (2004). Methods from various sources may not be consistent.

| | *dialuzona* | *spectabilis* | *octoactinotos* | *thiemmedhi* | *rungthipae* | *dinema* | *ioa* |
|---|---|---|---|---|---|---|---|
| No. specimens | 23 | 13 | 6 | 19 | 69 | 27 | 18 |
| No. pairs exposed labial barbels | 3 (rarely 0–2) | 2–3 | 2 | 1 (rarely 2) | 0 | 2 (rarely 3) | 0 |
| Black spot/ocellus on upper margin of caudal-fin base | Ocellus | Absent | Distinct spot | Absent | Distinct spot | Absent | Absent |
| Black pigment on dorsal fin | 4–5 bands; no large spots | Small black spot near tip of fin; 2–3 bands on fin | 1–2 faint bands; no large spots | Large black blotch on tip of fin; 2–3 bands on fin | 2–3 faint bands; no large spots | 2–3 faint bands; no large spots | 1–2 faint bands; no large spots |
| Black pigment on caudal fin | 4–5 bands; no large spots | 3–4 black spots on upper lobe, 2–3 larger spots on lower lobe | 1–2 faint bands; no large spots | 1 large black blotch on each lobe; smaller spots in middle | 4–5 bands; no large spots | Dark stripe on lower margin | 4–5 faint bands; no large spots |
| Dark pigment beneath midlateral row of black spots | Rarely black specks | No | No | No | Rarely black specks anteriorly | Dark pigment present | No |
| Dark pigment on side of head | 1–2 rows of large spots | 2–3 rows of large spots | No large spots | 1 row of large spots | 1 row of large spots | No large spots | 0–1 row of large spots |
| No. branched dorsal-fin rays | 10½ (rarely 9½,) | 9½ (rarely 8½) | 8½ (rarely 7½, 9½*) | 10½ (rarely 9½) | 9½ (rarely 10½) | 10½ | 9½ (rarely 10½) |
| No. pectoral-fin rays | 10 (rarely 9, 11) | 10 (rarely 11) | 9 (rarely 10) | 10 (rarely 9, 11) | 10 (rarely 9, 11) | 10 (rarely 9, 11) | 10 (rarely 9, 11) |
| No. dorsal saddles | 11–17 | 9–12 | 11–17 | 7–9 | 10–20 | 8–17 | 15–23 |
| No. midlateral spots | 7–13 | 9–15 | 8–13 | 6–10 | 9–17 | 6–12 | 13–21 |
| Total no. vertebrae | 42–43 | 43–44 | 41–42 | 39–41 | 41–43 | 41–42 | 46–48 |
| Total no. vertebrae, literature | 42–44* | — | 40–44* | 39–41* | — | — | — |
| Maximum SL, mm | 183.6 | 212.5 | 85.6 | 153.3 | 203.2 | 116.7 | 132.0 |

Bleeker (1860) described *A. dialuzona* as having irregular, diffuse, violet-colored spots in a longitudinal row or more or less united into a stripe along the side of the body, a small black spot at the upper edge of the caudal-fin base; and 3–4 dusky bands on the caudal fin.

**Distribution**. *Acantopsis dialuzona* occurs in Java, Borneo, Sumatra, and the Malay Peninsula as far north as southern Thailand (Fig. 7). This distribution primarily encompasses the Southern Sumatra-Western Java and Malay Peninsula Eastern Slope ecoregions of Abell *et al*. (2008). It has been reported from areas of Southeast Asia outside its range, including as *A. choirorhynchos* (e.g., Seibert 1991b, Sontirat 1999, and Vishwanath and Laisram 2005), because of the lack of taxonomic resolution in *Acantopsis*.

**Remarks**. *Cobitis choirorhynchos,* treated by Kottelat (2012) and here as a synonym of *A. dialuzona,* was described by Bleeker (1854) based on three specimens 170–178 mm in total length from Sumatra. Alfred (1961a) re-examined these specimens and designated a lectotype (RMNH 4977, Fig. 8) with a total length of 166 mm and SL of 142 mm (the shorter TL recorded by Alfred is presumably due to shrinkage). A more detailed description of *C. choirorhynchos* by Bleeker (1860) is reproduced in English in van Oijen and Loots (2012:75–76, fig. 3) along with an illustration from the "Atlas Ichthyologique" (Bleeker 1863–1864). The only characters used by Bleeker (1854, 1860) to distinguish *C. choirorhynchos* from *A. dialuzona* was a slightly longer head, going 4⅔ to slightly more than 5 times in length of the body vs. 5 to 5⅓ times in *A. dialuzona*; dark spots on the head, back, and side of the body vs. no dark spots on head and back; and anal fin with 5–6 rays vs. 6–7 rays. Head length increases with standard length, and the proportionally longer head in the type of *C. choirorhynchos* is a function of the fact that the type of *C. choirorhynchos* is larger than the type of *A. dialuzona* (Fig. 3). Presence/absence of dark pigment on the back and side of the body is highly variable and likely related to water clarity and the color of the substrate on which specimens were collected.



**FIGURE 8.** Lectotype of *Cobitis choirorhynchos*, RMNH 4977, 139.2 mm SL.

*Acantopsis spectabilis* **(Blyth, 1860)**
Spectacular Horseface Loach
(Fig. 9)

*Prostheacanthus spectabilis* Blyth, 1860: 167 (type locality: Burma: Tenasserim provinces; types: none known, possibly at ZSI but cannot be located [L. Kosygin, pers. comm., 6 Feb. 2017])
*Acantopsis spectabilis*.—Kottelat 2012:22
*Acantopsis multistigmatus* Vishwanath and Laisram, 2005: 433, fig. 1 (type locality: India: Manipur: Chindwin River basin, Lokchao stream, tributary of Yu River; holotype: MUMF 3044)

**Diagnosis.** *Acantopsis spectabilis* differs from all other species of *Acantopsis* (Table 4) by combination of 3–4 black spots along upper lobe, 2–3 larger, often darker, black spots on lower lobe of caudal fin (smaller black spots in middle of fin); 1–2 bands on anal and paired fins; 2–3 pairs of labial barbels, 9½ branched dorsal rays; 10 pectoral rays; 9–12 dark saddles along dorsal midline; 9–15 black spots along side of body; 2–3 rows of large dark spots on side of head, 43–44 total vertebrae, body depth 9.0–11.6% SL, body width 6.8–9.4% SL, caudal-peduncle length 12.9–16.6% SL.

**Comparisons.** The unique color pattern on caudal fin distinguishes *A. spectabilis* from all other species of *Acantopsis*. It is most similar to *A. thiemmedhi*, which differs in having 1 large black blotch on each lobe of caudal

fin. All other species of *Acantopsis* have no or dusky bands on caudal fin. It further differs from *A. thiemmedhi* by having 2–3 (vs. 1) pairs of labial barbels and in having usually 9½ (vs. 10½) branched dorsal rays and in lacking large black blotch on tip of anterior rays of dorsal fin. It further differs from *A. dinema* by having dark large spots on side of head, no row of black specks beneath midlateral row of black spots, usually 9½ (vs. 10½) branched dorsal rays, smaller body depth (9.0–11.6 vs. 12.0–14.5% SL). It further differs from *A. rungthipae* and *A. ioa* by having 2–3 (vs. 0) pairs of labial barbels, from *A. rungthipae* in lacking distinct small black spot on upper margin of caudal-fin base, and from *A. ioa* in having 9–12 (vs. 15–23) dark saddles along dorsal midline, 9–15 (vs. 13–21) black spots along side of body, large dark spots on side of head, 43–44 (vs. 46–48) total vertebrae. It further differs from *A. dialuzona* by lacking a well developed ocellus on the upper margin of the caudal-fin base and having usually 9½ (vs. 10½) branched dorsal rays.



**FIGURE 9.** *Acantopsis spectabilis.* (A) Lateral and dorsal views, CAS 238298, 163.0 mm SL. (B) Lateral views, CAS 88783, 112.9 mm SL and 56.2 mm SL.

**Description.** As in description of genus; Tables 1, 2, 4. Head long (21.8–25.7% SL); snout long (60.1–70.3% HL); 2–3 pairs of labial barbels; 9½, rarely 8½, branched dorsal rays; 10, rarely 11, pectoral rays; 31–32 abdominal + 12 caudal = 43–44 total vertebrae (N=3). Maximum SL = 212.5 mm, TL = 242.5 mm (NIFI 2456).

**Color.** Dark spots in 1 row on top of head, scattered or in 2–3 rows on side of head. Black line from eye to tip of snout. Nine–12 dark saddles along dorsal midline; 9–15 dark spots or blotches along to slightly below lateral line from head to caudal fin, varying from large and rounded to flattened and elongate; dark spots and blotches on

upper side of body, none on lower side. Two–3 bold, irregular bands of blotches on caudal fin, darkest at extremity of lower lobe and along margins. One–2 dark bands on anal and paired fins. Small black spot near tip of anterior rays of dorsal fin. No small black spot or ocellus near upper margin of caudal-fin origin.

**Distribution.** *Acantopsis spectabilis* is known from the Irrawaddy River basin of Myanmar and India, the Salween River basin of Thailand and Myanmar, and the Tenasserim provinces region (Dawei River, and presumably the Ataran River basin) of Myanmar (Fig. 10).
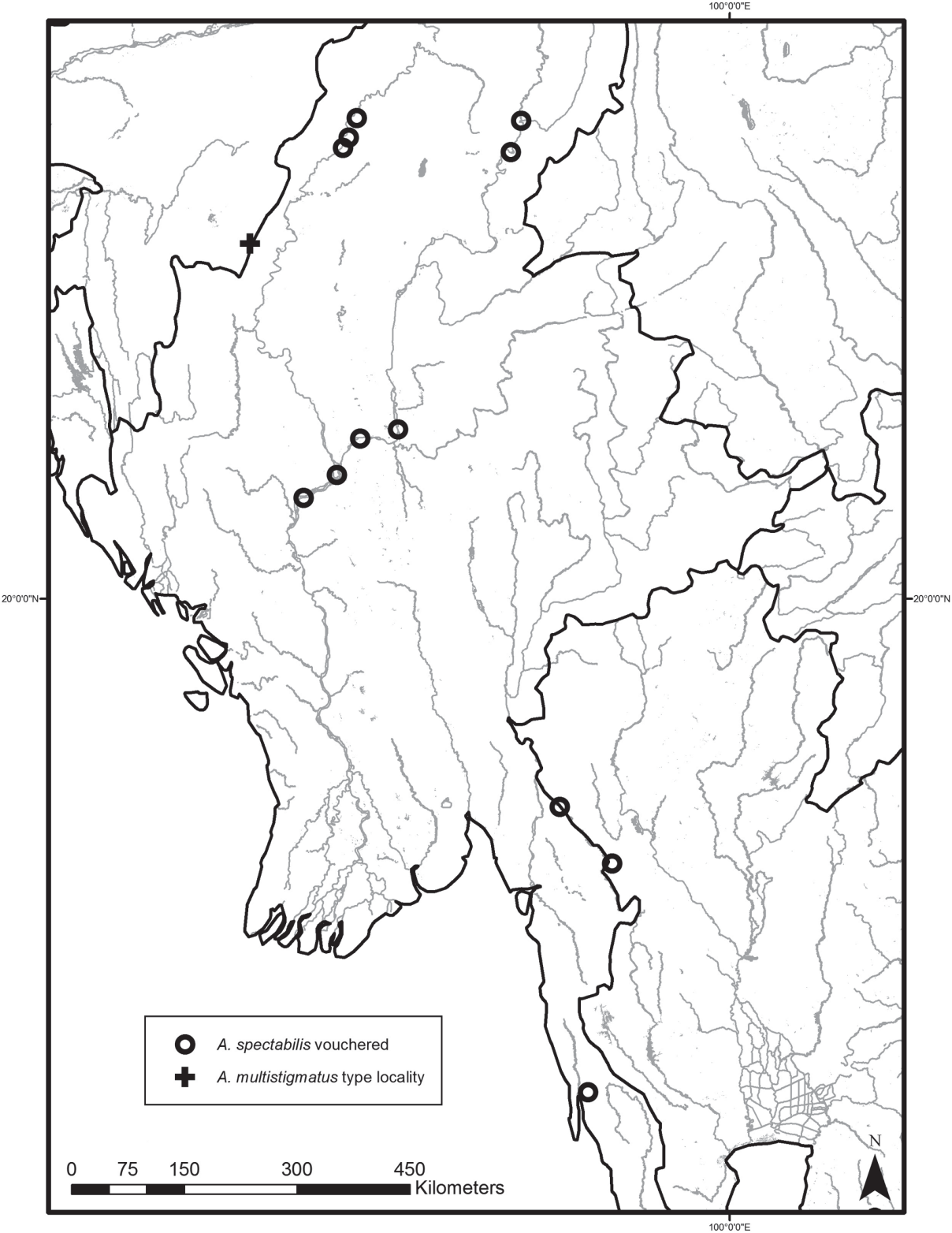


**FIGURE 10.** Localities of specimens examined of *Acantopsis spectabilis*, including the type locality of *A. multistigmatus*.

***Acantopsis octoactinotos*** Siebert, 1991
Dwarf Horseface Loach
(Fig. 11)

*Acantopsis octoactinotos* Siebert, 1991b: 910, fig. 2 (type locality: Malaysia: Borneo: Sabah: Kinabatangan District: tributary
of Kinabatangan River in lowlands near Deramakot River, approx. 5°18'N 117°33'E; holotype: FMNH 68148)

**Diagnosis.** *Acantopsis octoactinotos* differs from all other species of *Acantopsis* (Table 4) by having usually 8½ branched dorsal rays. It also differs by combination of 2 pairs of labial barbels, black spot on upper margin of caudal-fin base, no black spot on tip of anterior rays of dorsal fin, no large dark spots on side of head, no row of black specks beneath midlateral row of black spots, usually 9 pectoral rays, 11–17 dark saddles along dorsal midline, 8–13 large dark spots along side of body, 40–44 total vertebrae, body depth 9.6–11.2% SL, body width 6.8–7.9% SL, caudal-peduncle length 16.1–17.2% SL.

**Comparisons.** *Acantopsis octoactinotos* is distinguished from all other species of *Acantopsis* by having 8½ (vs. 9½ or 10½) branched dorsal rays, and all species except *A. dinema* by lacking large dark spots on side of head. It differs from *A. dialuzona, A. spectabilis, A. rungthipae,* and *A. ioa* in having 9 (vs. 10) pectoral rays, and from *A. spectabilis* and *A. thiemmedhi* in having black spot on upper margin of caudal-fin base and no conspicuous black spots, blotches, or bands on caudal fin. It further differs from *A. thiemmedhi* in lacking large black blotch on tip of anterior rays of dorsal fin, and in having 2 (vs. 1) pairs of labial barbels, 11–17 (vs. 7–9) dark saddles along dorsal midline, longer caudal-peduncle 16.1–17.2 vs. 12.5–14.7% SL. It further differs from *A. rungthipae* in having 2 (vs. 0) pairs of labial barbels; from *A. ioa* in having 2 (vs. 0) pairs of labial barbels, 8–13 (vs. 13–21) dark spots along side of body, 40–44 (vs. 46–48) total vertebrae; and from *A. dinema* in having a small black spot on upper margin of caudal-fin base, no row of black specks beneath midlateral row of black spots, smaller body depth 9.6–11.2 vs. 12.0–14.5% SL, longer caudal-peduncle 16.1–17.2 vs. 12.1–14.3% SL.



**FIGURE 11.** *Acantopsis octoactinotos.* Lateral and dorsal views, FMNH 68150, 72.3 mm SL.

**Description.** As in description of genus; Tables 1, 2, 4. Head long (22.5–24.6% SL); snout long (53.7–58.4% HL); 2 pairs of labial barbels; 8½ (rarely 7 or 9; Siebert 1991b) branched dorsal rays; 9, rarely 10, pectoral rays; 28–29 abdominal + 12–13 caudal = 41–42 total vertebrae (Table 1); Siebert (1991b) reported 40–44 total vertebrae. Maximum SL = 96.0 mm (FMNH 68150, caudal fin damaged).

**Color.** Dark spots in 1– 2 rows on top of head; no large dark spots on side of head. Black line from eye to tip of snout. Eleven–17 dark saddles along dorsal midline to origin of caudal fin; 8–13 dark spots or blotches along lateral line from head to caudal fin; small dark spots and reticulations on upper side of body; no dark spots on lower side of body below midlateral row of dark spots. Dorsal and caudal fins without bands; no dark margins on caudal fin. Small bold black spot near upper margin of caudal-fin origin; faint black spot on lower margin of caudal-fin origin. Inger and Chin (1962) reported pale yellowish coloration in live *A. octoactinotos*.

**Sexual dimorphism.** Males have a longer, ramified first branched pectoral-fin ray (Siebert 1991b).

BOYD *ET AL.*

**Distribution.** *Acantopsis octoactinotos* is known from the Kinabatangan River and Segama River (Martin-Smith and Tan 1998) basins, Sabah, Malaysia (Fig. 7).

## *Acantopsis thiemmedhi* Sontirat, 1999
Blackspotted Horseface Loach
(Fig. 12)

*Acantopsis thiemmedhi* Sontirat, 1999: 66, fig. 1 (type locality: Thailand: Uthai Thani Province: Amphoe Lan Sak: Huai Kha Khaeng Wildlife Sanctuary, Nam Khun Creek; holotype: KUMF 3131)
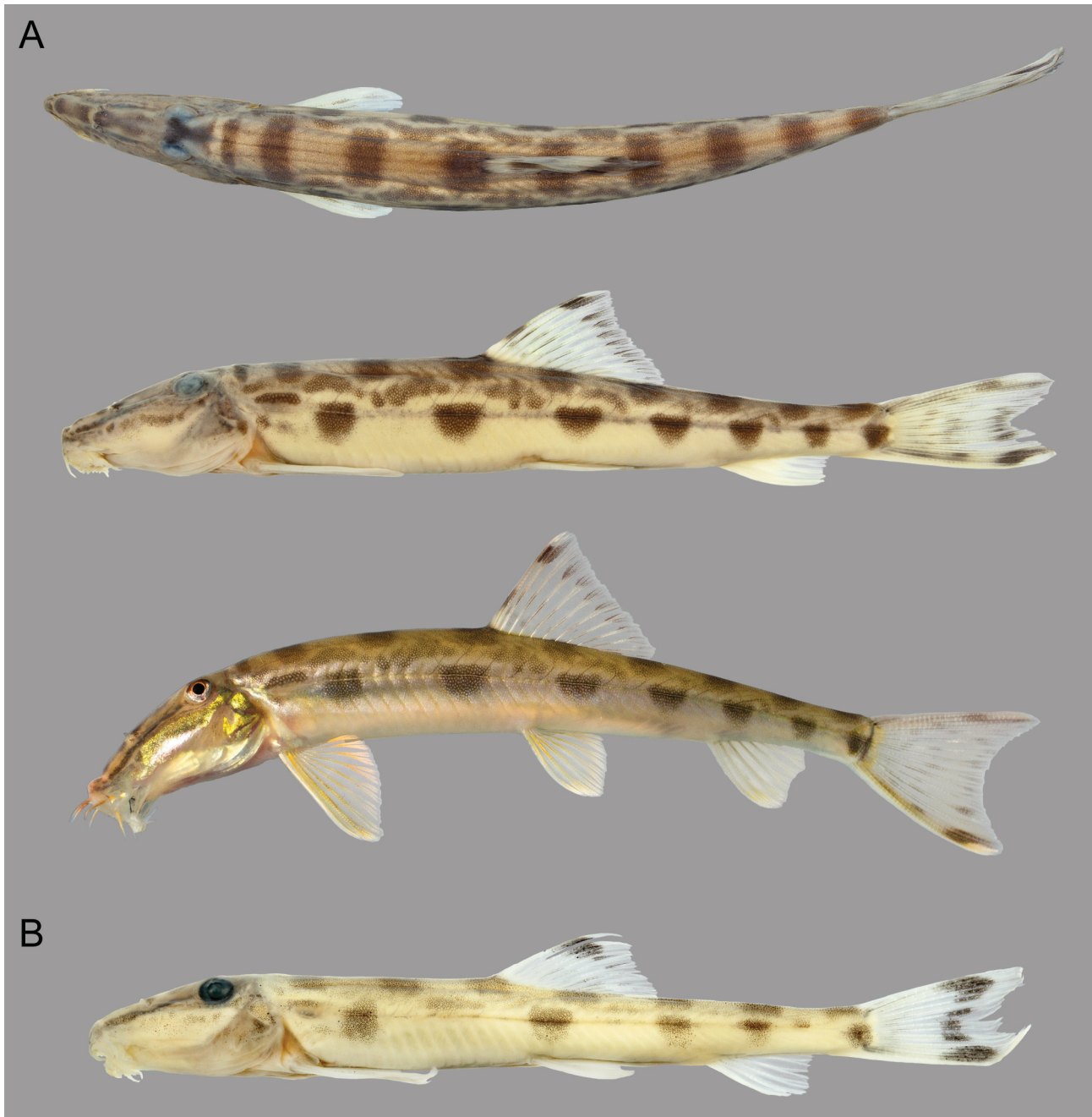


**FIGURE 12.** *Acantopsis thiemmedhi*, UF 188118. (A) Dorsal, lateral, and live views, 107.5 mm SL. (B) Lateral view, 54.5 mm SL.
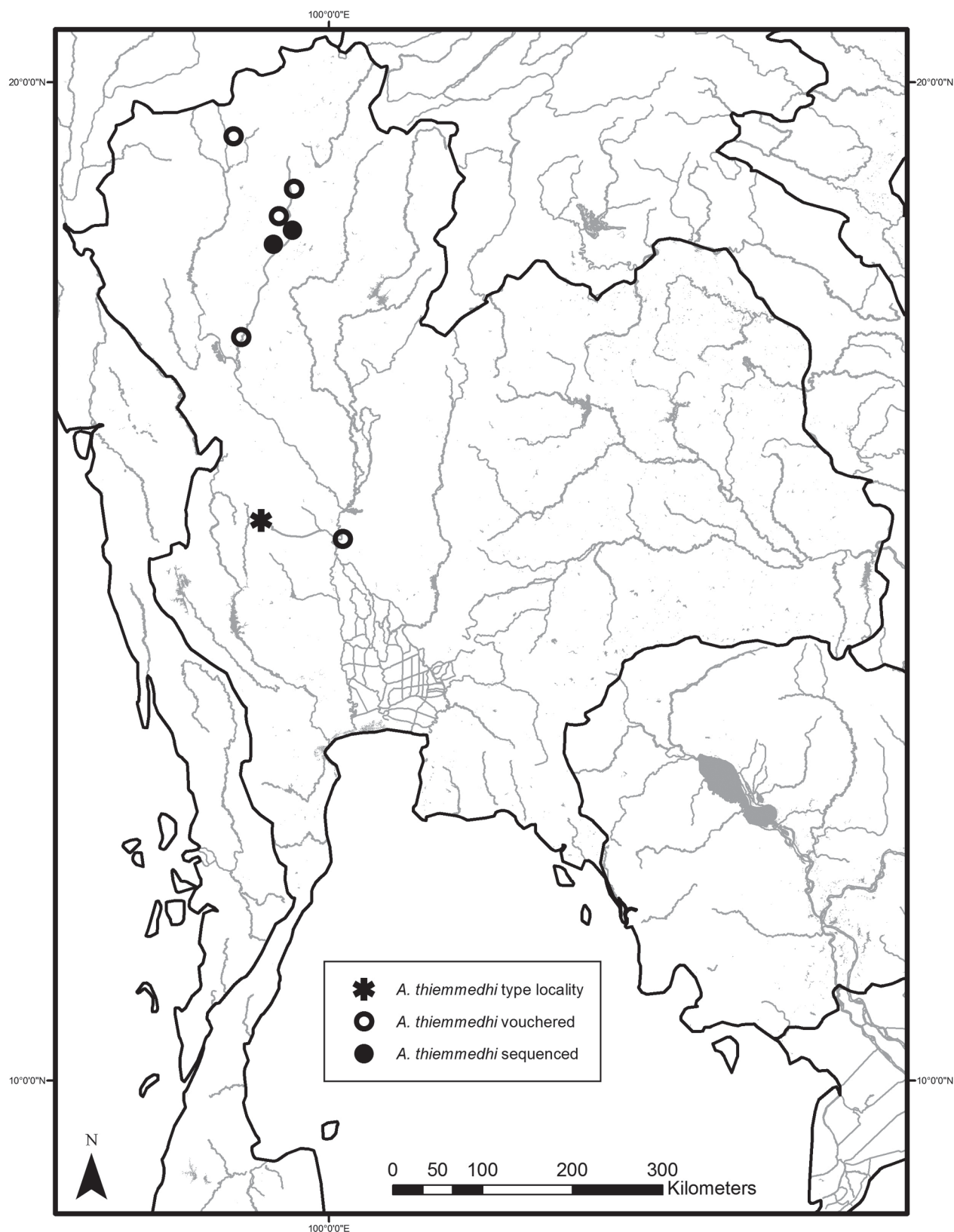
**FIGURE 13.** Localities of specimens examined of *Acantopsis thiemmedhi.*

**Diagnosis.** *Acantopsis thiemmedhi* differs from all other species of *Acantopsis* (Table 4) by combination of large black blotch on tip of anterior rays of dorsal fin, large black blotch on tip of each lobe of caudal fin; usually 1 pair of labial barbels, 10½ branched dorsal rays, and 10 pectoral rays; 7–9 dark saddles along dorsal midline, 6–10

black spots along side of body, 1 row of large dark spots on side of head, 39–41 total vertebrae, body depth 9.8–16.6% SL, body width 5.8–10.3% SL, caudal-peduncle length 12.5–14.7% SL.

**Comparisons.** *Acantopsis thiemmedhi* differs from all other species of *Acantopsis* by having large black blotch on tip of anterior rays of dorsal fin and large black blotch on each lobe of caudal fin. *Acantopsis spectabilis* has much smaller black blotch (often absent) on tip of anterior rays of dorsal fin, 2–3 irregular bands or blotches on caudal fin, darkest at extremity of lower lobe. Other species of *Acantopsis* have dusky to dark bands on dorsal fin but no conspicuous black blotch at tip of anterior rays, and dusky bands on caudal fin. *Acantopsis thiemmedhi* further differs from *A. spectabilis* in having 1 (vs. 2–3) pair of labial barbels, and usually 10½ (vs. 9½) branched dorsal rays. *Acantopsis thiemmedhi* further differs from *A. dialuzona* by lacking well developed ocellus on the upper margin of the caudal-fin base, and having 1 (vs. 3) pair of labial barbels, 7–9 (vs. 11–17) dark saddles along dorsal midline, and 6–10 (vs. 7–13) black spots along side of body. It further differs from *A. octoactinotos* by having usually 10½ (vs. 8½) branched dorsal rays, large dark spots on side of head, 1 (vs. 2) pair of labial barbels, usually 10 (vs. 9) pectoral rays, 7–9 (vs. 11–17) dark saddles along dorsal midline, shorter caudal-peduncle 12.5–14.7 vs. 16.1–17.2% SL. It further differs from *A. dinema* by having 1 (vs. 2) pair of labial barbels, large dark spots on side of head, and no row of black specks beneath midlateral row of black spots. It further differs from *A. rungthipae* and *A. ioa* by having 1 (vs. 0) pair of labial barbels and usually 10½ (vs. 9½) branched dorsal rays, from *A. rungthipae* in lacking distinct small black spot on upper margin of caudal-fin base and in having 6–10 (vs. 9–17) black spots along side of body, and from *A. ioa* in having 7–9 (vs. 15–23) dark saddles along dorsal midline, 6–10 (vs. 13–21) black spots along side of body, large dark spots on side of head, 39–41 (vs. 46–48) total vertebrae.

**Description.** As in description of genus; Tables 1, 2, 4. Head long (22.6–26.8% SL); snout long (57.5–68.3% HL); 1, rarely 2, pairs of labial barbels; 10½, rarely 9½ or 11½, branched dorsal rays; 10, less often 9 or 11, pectoral rays; 28–30 abdominal + 10–11 caudal = 39–41 total vertebrae (Table 1; Sontirat 1999). Maximum SL = 153.3 mm, TL = 191.5 mm (NIFI 2974).

**Color.** Dark spots in 1 row on top of head, in 1–2 often poorly defined rows on side of head. Black line from eye to tip of snout. Seven–9 dark saddles along dorsal midline; 6–10 large dark spots or blotches along lateral line from head to caudal fin; dark spots and blotches on upper side of body, none on lower side. Large black blotch near tip of anterior rays of dorsal fin, separated from black band near margin of fin; large individuals with second band in middle of fin with black spot anteriorly. Large black blotch on each lobe of caudal fin, sometimes with dark band connecting blotches; often smaller black spots or bands in middle of caudal fin. Faint bands on other fins. No small bold black spot or ocellus near upper margin of caudal-fin origin.

Live individuals yellowish brown dorsally, white below, with large black blotches dorsally and laterally on body; dorsal and caudal fins with black and white bands and spots, iridescent yellow on side of head and lower fins.

**Distribution.** *Acantopsis thiemmedhi* is widespread, but seemingly uncommon, in the Chao Phraya River basin, Thailand (Fig. 13). Most of the specimens examined are from the Wang River drainage.

**Remarks.** The holotype of *Acantopsis thiemmedhi,* KUMF 3131, was examined and found to differ in fin ray counts from those recorded by Sontirat (1999). It has 9 branched dorsal rays, 11 pectoral rays, and 7 pelvic rays. Pectoral-fin rays for all 21 paratypes range from 9 to 11.


***Acantopsis rungthipae* new species, Boyd, Nithirojpakdee, and Page**
Piebald Horseface Loach
(Fig. 14)

**Holotype**. THNHM F0013610, 107.4 mm SL female (ex. UF 235976), Thailand, Welu River drainage, Chanthaburi Province, Khlung District, Khen Creek, tributary of Trok Nong River, off Rt. 3277, 12.537N, 102.244E, 30 January 2014, Nithirojpakdee, J. *et al.*

**Paratypes**. Thailand: Welu River drainage: same locality and date as holotype: UF 235976 (6, 89.9–119.7 mm SL); ZRC 55596 (2, 93.2–111.6 mm SL); NIFI 5102 (2, 94.2–118.0 mm SL). Tapi River drainage: ANSP 179976 (1, 119.0 mm SL), Krabi/Surat Thani Provinces, Ipan River, trib. of Tapi River, on Rt. 4035, 25 km NE of Ao Luek, 08.623N, 98.980E, 22 February 2001, M. H. Sabaj and M. Hardman. INHS 93550 (1, 109.0 SL) same locality and date as ANSP 179976.
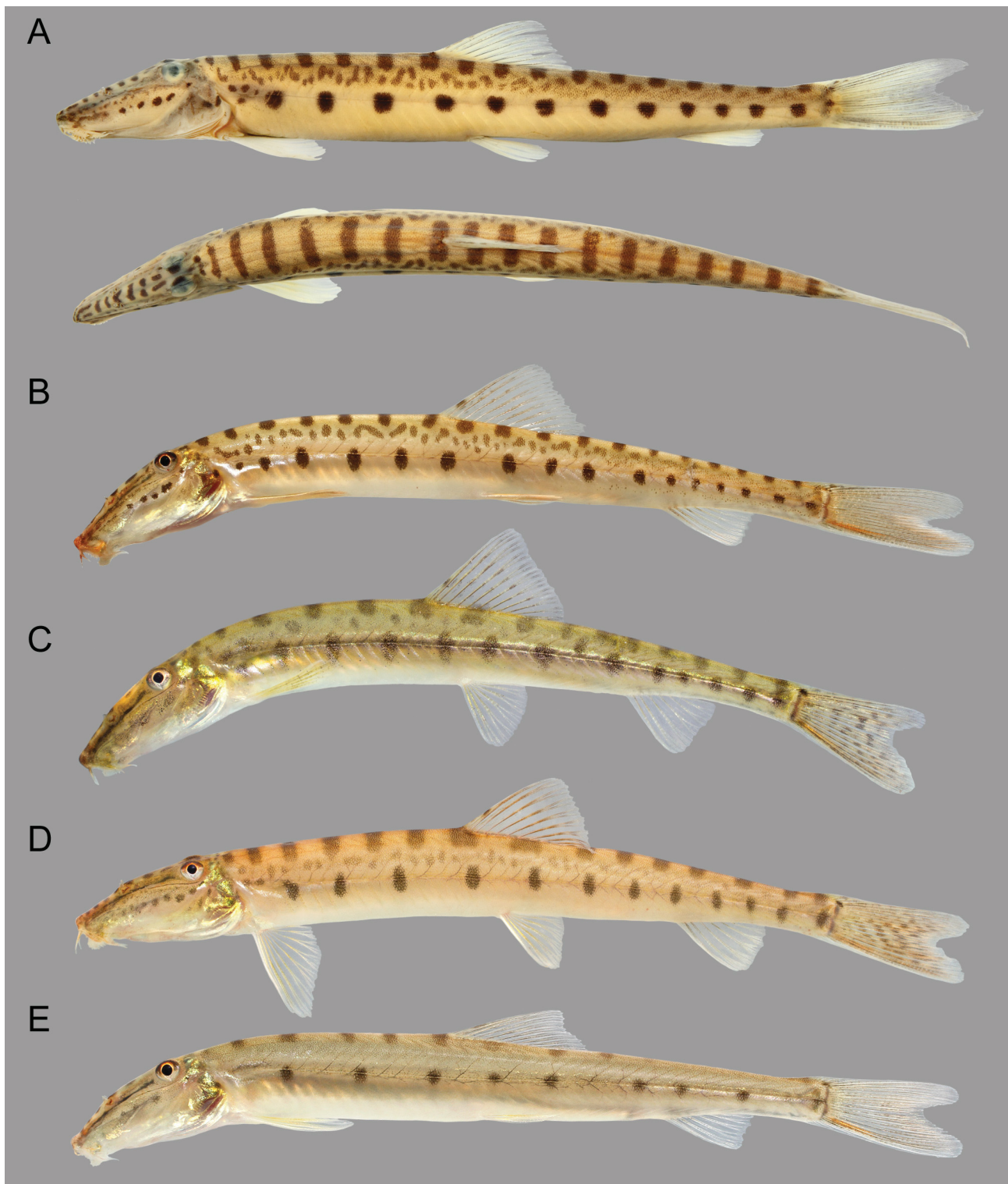
**FIGURE 14.** *Acantopsis rungthipae*. (A) Lateral and dorsal views, THNHM F0013610, holotype, Welu River, 107.4 mm SL. Live views of (B) UF 235976, paratype, Welu River, 91.7 mm SL, (C) UF 188117, Wang River, 56.4 mm SL, (D) UF 188114, Songkhram River, 90.6 mm SL, and (E) UF 236085, Tapi River, 77.3 mm SL.

**Diagnosis.** *Acantopsis rungthipae* differs from all other species of *Acantopsis* (Table 4) by combination of no exposed labial barbels, usually distinct small black spot on upper margin of caudal-fin base, 0–1 row of large spots on side of head, no large black spots on dorsal or caudal fins, no black specks beneath midlateral row of black spots (rarely present), usually 9½ branched dorsal rays and 10 pectoral rays, 10–20 dark saddles along dorsal midline, 9–17 black spots along side of body, 41–43 total vertebrae, body depth 9.0–14.2% SL, body width 5.3–10.3% SL, caudal-peduncle length 11.5–16.1% SL.

**Comparisons.** *Acantopsis rungthipae* is distinguished from all species of *Acantopsis* except *A. ioa* by having no labial barbels. It is distinguished from *A. ioa* by usually having a distinct small black spot on upper margin of caudal-fin base, 9–17 (vs. 13–21) black spots along side of body, and 41–43 (vs. 46–48) total vertebrae (Fig. 15). It further differs from *A. dinema* by having large dark spots on side of head, usually lacking conspicuous row of black specks beneath midlateral row of black spots, having usually 9½ (vs. 10½) branched dorsal rays, a distinct small black spot (vs. no spot) on upper margin of caudal-fin base, and usually 4–6 faint, narrow bands (vs. no bands) on caudal fin. It further differs from *A. octoactinotos* by having usually 9½ (vs. 8½) branched dorsal rays, large dark spots on side of head, usually 10 pectoral rays. It differs from *A. spectabilis* and *A. thiemmedhi* in lacking conspicuous black bands on the anal and paired fins and spots or blotches on the caudal fin. It further differs from *A. thiemmedhi* in lacking a large black blotch on the tip of the anterior rays of the dorsal fin and in having usually 9½ (vs. 10½) branched dorsal rays, and from *A. dialuzona* by lacking a well developed ocellus on the margin of caudal-fin base and having usually 9½ (vs. usually 10½) branched dorsal rays.
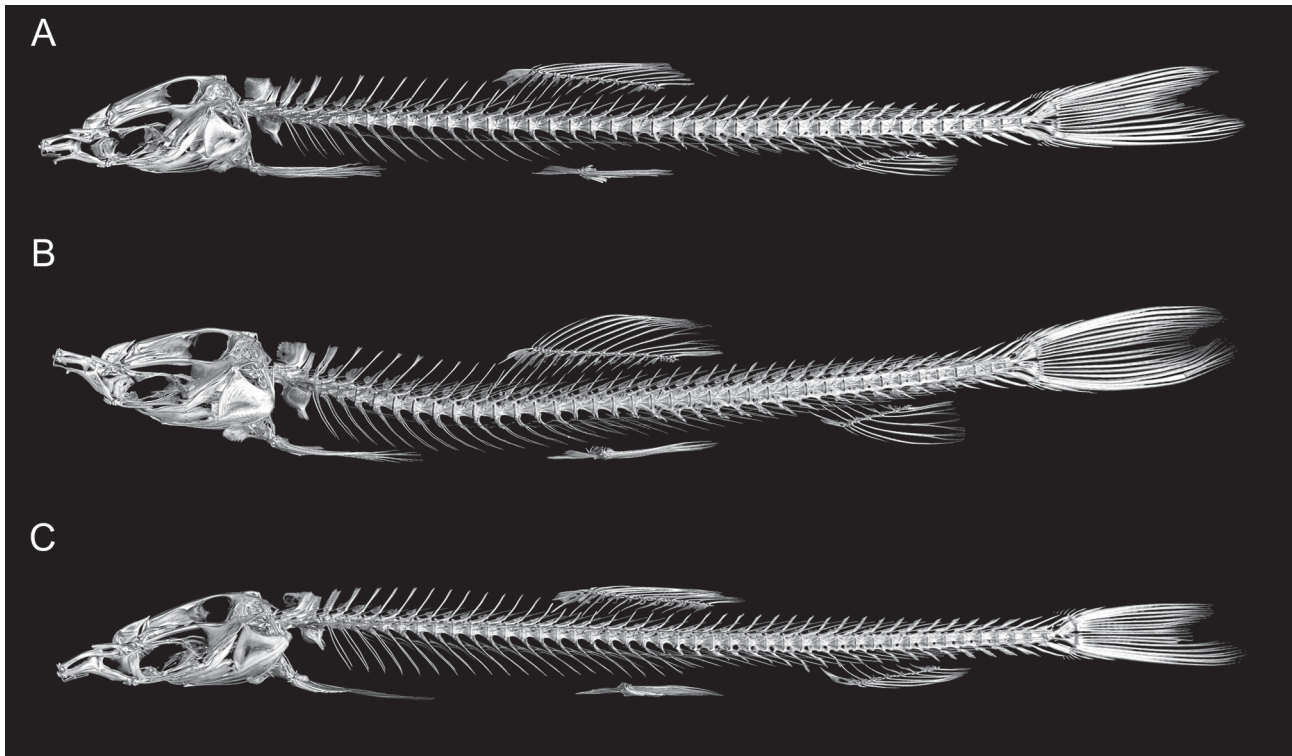


**FIGURE 15.** CT-scans of (A) *Acantopsis rungthipae*, THNHM F0013610, holotype, 107.4 mm SL. (B) *A. dinema*, THNHM F0013611, holotype, 100.7 mm SL. (C) *A. ioa*, UF 188136, 95.5 mm SL. CT-scans provided by E. L. Stanley (UF).

**Description.** As in description of genus; Tables 1, 2, 4. Head long (21.6–25.6% SL); snout long (54.7–68.7% HL); no exposed labial barbels; 9½, rarely 10½, branched dorsal rays; 10, rarely 9 or 11, pectoral rays; 29–31 abdominal + 11–12 caudal = 41–43 total vertebrae. Maximum SL = 203.2 mm, TL = 241.3 mm (CAS 238293).

**Color.** Dark spots in 1–2 rows on top of head, usually 1 row anteriorly, 2 posteriorly; dark spots on side of head usually in 1 row. Black line from eye to tip of snout. Ten–20 dark saddles along dorsal midline; 9–17 large dark spots or blotches along lateral line from head to caudal fin; small dark spots on upper side of body; no or few dark spots on lower side of body below midlateral row of dark spots. Dorsal fin with 2–3 faint bands, caudal with 4–5 faint bands; no dark upper and lower margins on caudal fin. Small bold black spot near upper margin of caudal-fin origin.

Live individuals yellowish brown dorsally, white below, with large black blotches dorsally and laterally on body; reddish brown streak on lower caudal margin; iridescent yellow on side of head and lower fins.

**Sexual dimorphism.** Males have a longer, ramified first branched pectoral-fin ray.

**Etymology.** This species is named in honor of Rungthip Plongsesthee, who was born on 27 May 1978 and died on 16 July 2014. "Kae" was a dear friend, close colleague, a Ph.D. student of Dr. F. W. H. Beamish at Burapha University, Bangsaen, Thailand, and an extremely enthusiastic ichthyologist who is greatly missed by her many friends.

**Distribution.** *Acantopsis rungthipae* is the most widespread and common species of *Acantopsis* in mainland Asia. It is known from the Tapi, Mae Khlong, Chao Phraya, Bang Pakong, and Welu River basins in Thailand, and the Mekong River basin in Thailand, Cambodia, Laos, and Vietnam (Fig. 16).
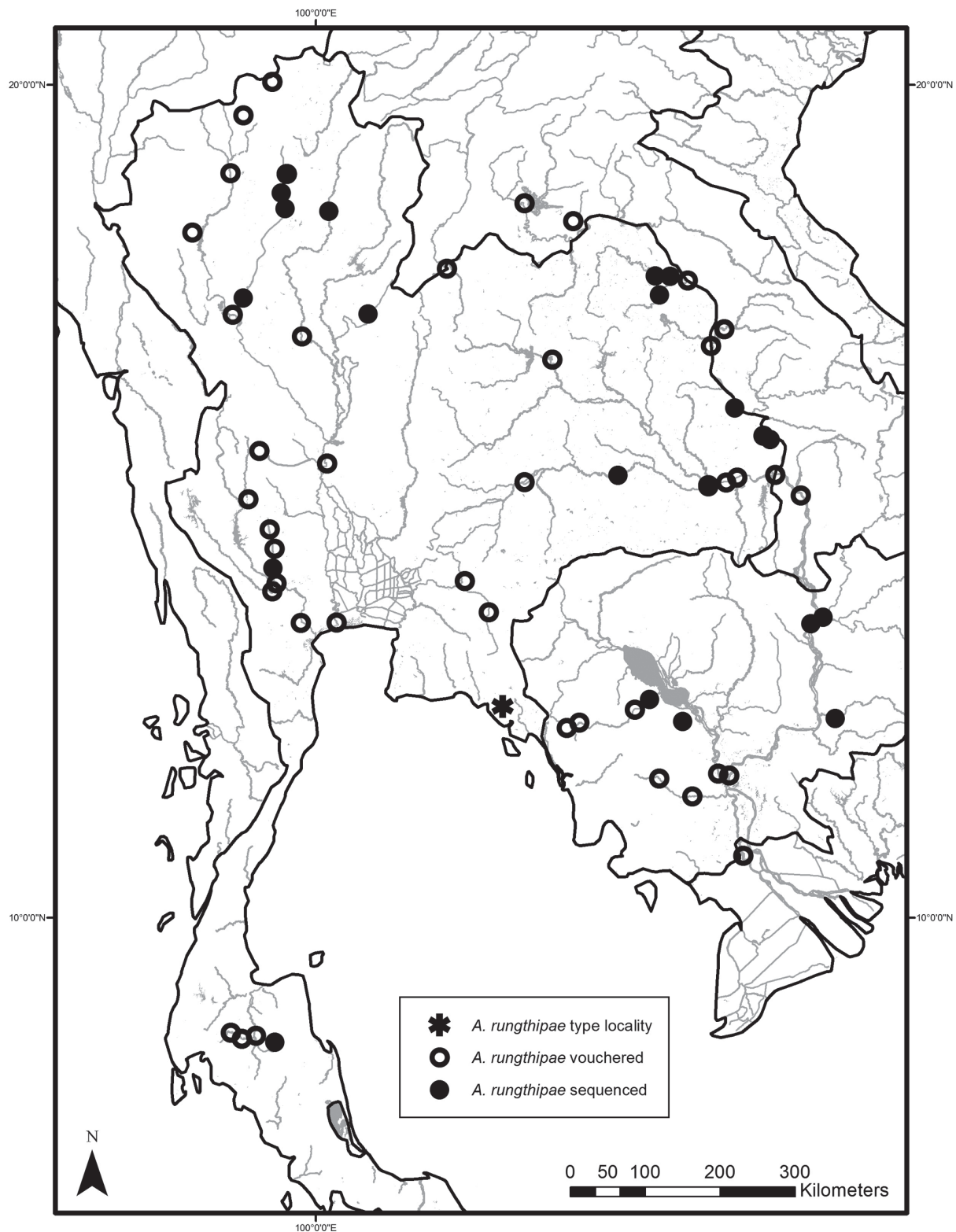


**FIGURE 16.** Localities of specimens examined of *Acantopsis rungthipae*.

## *Acantopsis dinema* new species, Boyd and Page
Peppered Horseface Loach
(Fig. 17)

**Holotype**. THNHM F0013611, 100.7 mm SL female (ex. UF 188225), Thailand, Mekong River drainage, Ubon Ratchathani Province, Pho Sai District, Ta Wang River on Rt. 2112, 4 km S of Rt. 2337, 15.793N, 105.376E, 1 February 2016, Randall, Z. *et al*.



**FIGURE 17.** *Acantopsis dinema*. A) Lateral and dorsal views, UF 188116, paratype, Songkhram River, 118.3 mm SL. Live views of (B) UF 188116, paratype, Songkhram River, 111.8 mm SL, (C) UF 188225, paratype, Ta Wang River, 72.8 m SL, and (D) UF 188111, Mun River, 89.7 mm SL.
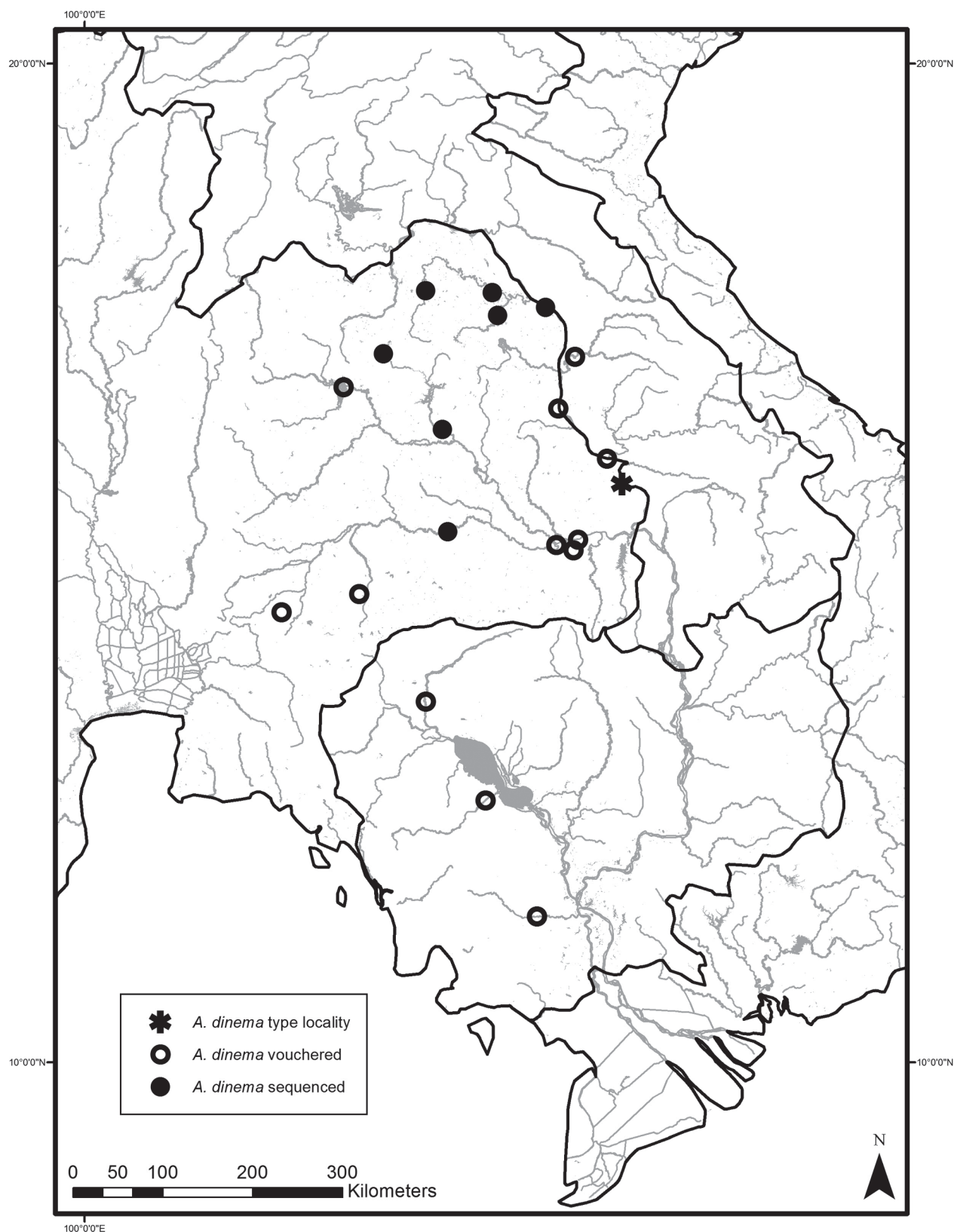
**FIGURE 18**. Localities of specimens examined of *Acantopsis dinema.*

**Paratypes**. Thailand: Mekong River drainage: UF 188225 (3, 72.4–97.9 mm SL), same locality and date as holotype. UF 185131 (9, 71.5–94.3 mm SL), same locality as holotype, 3 January 2013, Singer, R. *et al.* ANSP 200533 (2, 89.5–90.9 mm SL), ex. UF 185131. NIFI 5104 (2, 81.0–86.9 mm SL), ex. UF 185131. UF 188116 (56,

68.1–117.7 mm SL), Sakon Nakhon Province, Akat Amnuai District, Songkhram River at confluence with Yam River, 17.709N, 104.076E, 8 January 2015, Boyd, D. *et al.* ZRC 55598 (3, 94.6–105.5 mm SL), ex. UF 188116. INHS 110606 (3, 75.8–107.7 mm SL), ex. UF 188116.

**Diagnosis.** *Acantopsis dinema* differs from all other species of *Acantopsis* (Table 4) by combination of no large spots on side of head, many black specks beneath midlateral row of black spots from head to caudal fin, 2 pairs of labial barbels, no distinct small black spot on upper margin of caudal-fin base, no large black spots on dorsal or caudal fins, usually 10½ branched dorsal rays and 10 pectoral rays, 8–17 dark saddles along dorsal midline, 6–12 black spots along side of body, 41–42 total vertebrae, body depth 12.0–14.5% SL, body width 8.0–10.3% SL, caudal-peduncle length 12.1–14.3% SL.

**Comparisons.** *Acantopsis dinema* is distinguished from all other species of *Acantopsis* by having a row of black specks beneath midlateral row of black spots (specks rarely present in *A. dialuzona* and *A. rungthipae*; absent in other species of *Acantopsis*), and from all species except *A. octoactinotos* by having no dark spots on side of head (vs. usually conspicuous dark spots or specks on side of head). It further differs from *A. rungthipae* and *A. ioa* by having 2 (vs. 0) pairs of labial barbels, usually 10½ (vs. 9½) branched dorsal rays; from *A. rungthipae* by lacking distinct small black spot on upper margin of caudal-fin base; and from *A. ioa* in having 6–12 (vs. 13–21) black spots along side of body, 41–42 (vs. 46–48) total vertebrae (Fig. 15), a wider body (8.0–10.3 vs. 5.2–7.9% SL). It further differs from *A. octoactinotos* in having usually 10½ (vs. 8½) branched dorsal rays, usually 10 (vs. 9) pectoral rays, no small black spot on upper margin of caudal-fin base, a shorter caudal peduncle (12.1–14.3 vs. 16.1–17.2% SL). It further differs from *A. spectabilis* and *A. thiemmedhi* in lacking conspicuous black spots, blotches, or bands on caudal, anal, and paired fins; from *A. spectabilis* in having usually 10½ (vs. 9½) branched dorsal rays; and from *A. thiemmedhi* in having 2 (vs. 1) pairs of labial barbels, no large black blotch on tip of anterior rays of dorsal fin. It further differs from *A. dialuzona* in having 2 (vs. 3) pairs of labial barbels, no well developed ocellus on upper margin of caudal-fin base. It differs from *A. dialuzona, A. spectabilis, A. octoactinotos,* and *A. ioa* by having a deeper body (12.0–14.5 vs. 8.9–11.9, 9.0–11.6, 9.6–11.2, and 8.5–11.0% SL, respectively).

**Description.** As in description of genus; Tables 1, 2, 4. Head long (24.1–26.9% SL); snout long (58.8–65.9% HL); 2, rarely 3, pairs of labial barbels; 10½, rarely 11½, branched dorsal rays; 10, less often 9 or 11, pectoral rays; 29–31 abdominal + 10–13 caudal = 41–42 total vertebrae. Maximum SL = 116.7 mm, TL = 139.1 mm (UF 188116).

**Color.** Dark spots in 1 or 2 rows on top of head; no or few scattered small spots on side of head; none large. Black line from eye to tip of snout. Eight–17 dark saddles along dorsal midline to origin of caudal fin; 6–12 large dark spots or blotches along lateral line from head to caudal fin; many small dark spots or specks on upper side of body and on lower side of body just below midlateral row of dark spots from head to caudal fin. Fins usually without obvious bands; 2–3 faint bands on dorsal fin of large individuals. Dark upper and lower margins of caudal fin. No small bold black spot or ocellus near upper or lower margins of caudal-fin origin. Live individuals yellowish brown dorsally, white below, with large black blotches dorsally and laterally on body; iridescent yellow on side of head and lower fins.

**Sexual dimorphism.** Males have a longer first branched pectoral-fin ray, ramified and with a distinctive lateral lobe on the distal end (Fig. 5). As far as is known, other species of *Acantopsis* do not develop the distinctive distal expansion of the first branched pectoral-fin ray. In the largest series of *A. dinema* examined, (UF 188116) males (N = 15) averaged 88.1 mm SL, and females (N = 45) averaged 99.5 mm SL.

**Etymology.** The epithet *dinema*, from Latin, *di* meaning two, and *nema*, for thread, refers to the usual presence of two pairs of labial barbels in this species.

**Distribution.** *Acantopsis dinema* is widespread and common in the tributaries of the Mekong River draining the Khorat Plateau and Mekong Delta ecoregions (Abell *et al.* 2008) in Thailand, Laos, and Cambodia (Fig. 18), from the Songkhram River in eastern Thailand to the Prek Thnot River south of Phnom Penh, Cambodia.


*Acantopsis ioa* **new species, Boyd and Page**
Slender Horseface Loach
(Fig. 19)

**Holotype.** UMMZ 250301, 128.4 mm SL (ex. UMMZ 240684), Laos, Mekong River drainage, Vientiane Province, Nam Lik, 6 km upstream of confluence with Nam Ngum River, 18.583N, 102.500E, 22 January 1997, W. J. Rainboth and M. Anderson.

**Paratypes**. Laos: Mekong River drainage: UMMZ 240684 (13, 88.4–132.0 mm SL), same locality and date as holotype. UF 190865, 3, 96.5–114.9 mm SL (ex. UMMZ 240684). THNHM F0013612, 1, 107.1 mm SL (ex. UMMZ 240684). Thailand: Mekong River drainage: UF 188135 (23, 60.6–98.4 mm SL), Ubon Ratchathani Province, Khong Chiam District, Mekong River at mouth of Mun River, 15.318N, 105.513E, 22 January 2015, D. Gridsada *et al*.; ANSP 200532 (2, 78.8–79.0 mm SL), ex. UF 188135; NIFI 5103 (2, 72.2–73.3 mm SL), ex. UF 188135; ZRC 55597 (2, 80.2–82.8 mm SL), ex. UF 188135; INHS 110605 (2, 82.7–83.6 mm SL), ex. UF 188135.

**Diagnosis**. *Acantopsis ioa* differs from all other species of *Acantopsis* (Table 4) by combination of no labial barbels, usually no distinct small black spot on upper margin of caudal-fin base, 0–1 row of large spots on side of head, no large black spots on dorsal or caudal fins, no row of black specks beneath midlateral row of black spots, usually 9½ branched dorsal rays and 10 pectoral rays, 15–23 narrow, blotch-like saddles along dorsal midline, 13–21 black spots along side of body, and 46–48 total vertebrae, body depth 8.5–11.0% SL, body width 5.2–7.9% SL, caudal-peduncle length 13.1–16.2% SL.



**FIGURE 19.** *Acantopsis ioa.* (A) Lateral view, UMMZ 250301, holotype, 128.4 mm SL. (B) Lateral and dorsal views, UMMZ 240684, paratype, 131.0 mm SL.

**Comparisons**. *Acantopsis ioa* is distinguished from all species of *Acantopsis* by having narrow blotch-like dorsal saddles, 46–48 (vs. <45) total vertebrae (Fig. 15), and from all other species in the genus except *A. rungthipae* by having no labial barbels. It is further distinguished from *A. rungthipae* by usually lacking a distinct small black spot on upper margin of caudal-fin base, 13–21 (vs. 9–17) black spots along side of body. It further differs from *A. dinema* in having no black specks beneath midlateral row of black spots, large dark spots usually present on side of head, usually 9½ (vs. 10½) branched dorsal rays, smaller body depth (8.5–11.0 vs. 12.0–14.5% SL) and width (5.2–7.9 vs. 8.0–10.2% SL). It further differs from *A. octoactinotos* in having no distinct small black spot on upper margin of caudal-fin base, large dark spots usually present on side of head, usually 9½ (vs. 8½) branched dorsal rays, usually 10 (vs. 9) pectoral rays. It further differs from *A. spectabilis* and *A. thiemmedhi* in lacking conspicuous black spots, blotches, or bands on caudal, anal, and paired fins and in having 15–23 (vs. <13) dark saddles along dorsal midline, from *A. thiemmedhi* in lacking a large black blotch on the tip of the anterior rays of the dorsal fin and in having usually 9½ (vs. 10½) branched dorsal rays, and from *A. dialuzona* by lacking a well developed ocellus on upper margin of caudal-fin base and having usually 9½ (vs. 10½) branched dorsal rays.
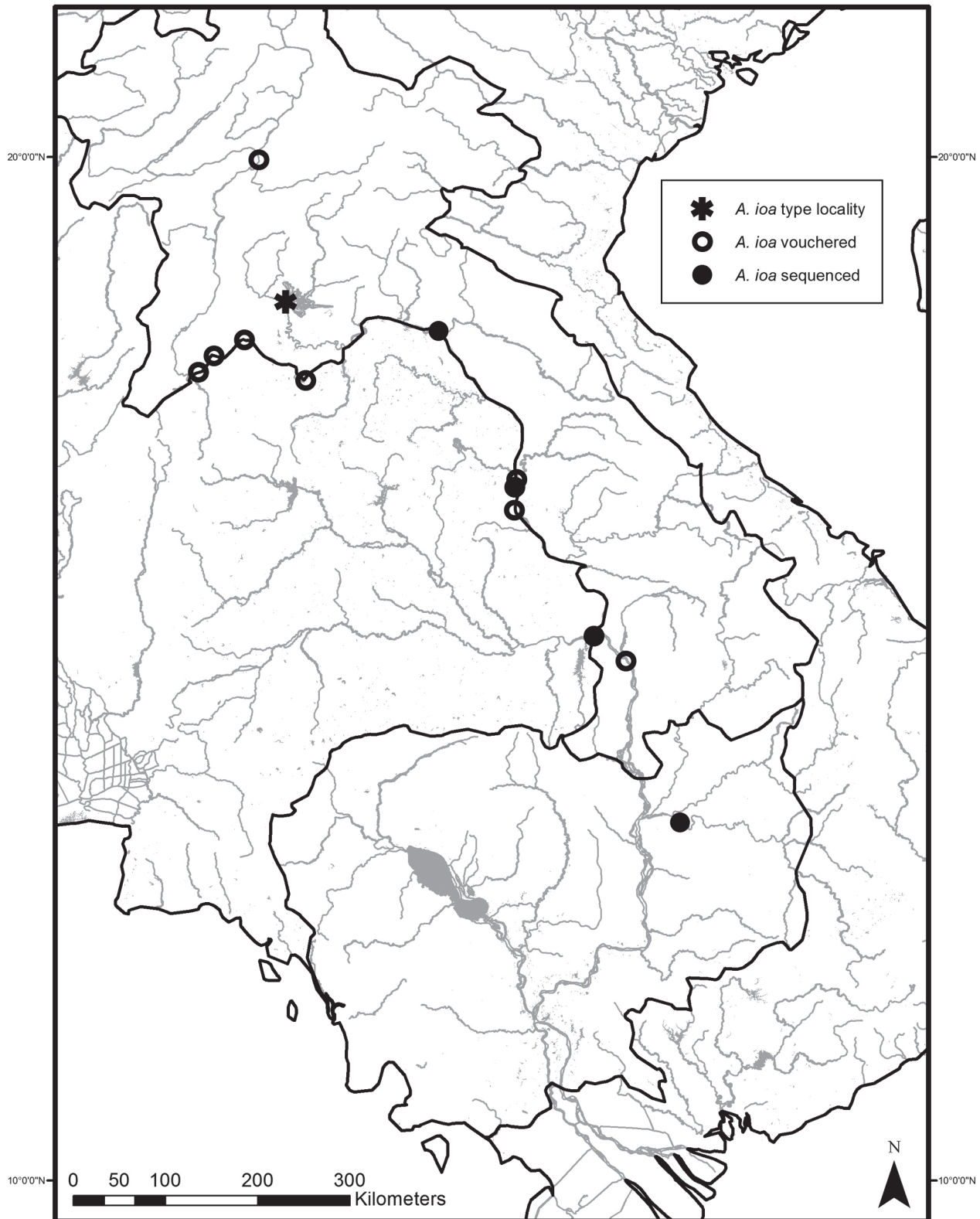
**FIGURE 20**. Localities of specimens examined of *Acantopsis ioa*.

**Description.** As in description of genus; Tables 1, 2, 4. Head long (21.8–24.2% SL); snout long (61.0–69.6% HL); no exposed labial barbels; 9½, rarely 10½, branched dorsal rays; 10, less often 9 or 11, pectoral rays; 33–35 abdominal plus 13–14 caudal = 46–48 total vertebrae. Maximum SL = 132.0 mm, TL = 152.9 mm (UMMZ 240684).

**Color.** Dark spots in 1 or 2 rows on top of head. Few large dark spots on side of head; if present, usually in 1 row. Faint line from eye to tip of snout. Fifteen–23 narrow, rounded saddles along dorsal midline; 13–21 dark spots along lateral line from head to caudal fin; spots more discrete than in other species. Small dark spots on upper side of body; no dark spots on lower side of body. Dorsal and caudal fins with faint bands; other fins without bands. Often a dusky stripe on lower margin of caudal fin. No small bold black spot (rarely present) or ocellus near upper margin of caudal-fin origin.

**Etymology.** The epithet *ioa*, from Greek for an arrow or dart, refers to the relative slenderness of this species in relation to other species of *Acantopsis*.

**Distribution.** *Acantopsis ioa* is widespread in the mainstem Mekong River in Thailand and Laos (Fig. 20). It also is known from the Nam Lik, a large tributary of the Mekong in Laos, and the Srepok River, a large tributary of the Mekong in Cambodia.

## Discussion

Considering the long-standing lack of taxonomic resolution among species of *Acantopsis*, especially those from mainland Southeast Asia, the phylogenetic analyses revealed surprisingly high molecular divergence between species. Uncorrected p-distances in the mitochondrial marker *CO1* ranged from 12.1 to 15.4% (Table 3), suggesting that even those species which display significant overlap of highly variable morphological traits have long been isolated from one another. Several species, especially *A. ioa, A. dialuzona,* and *A. rungthipae*, show interesting geographic structure in the molecular data (Fig. 4) that should be explored further for historical and ecological explanations.

Previously published molecular data (*RAG1* and cyt*b*) indicated that *Acantopsis* is sister to a clade containing *Aperioptus* (reported as *Acanthopsoides*) and *Kottelatlimia* (Šlechtová *et al.* 2008, Havird *et al.* 2010). However, our analysis of *RAG1* and *CO1* suggests that *Aperioptus* is sister to *Acantopsis* plus *Kottelatlimia*. This may be the result of more outgroup taxa in the earlier studies, a greater diversity of samples of *Acantopsis* in the present study, or the variation in mitochondrial loci examined. More samples, taxa, and loci are needed to resolve the suprageneric relationships of these taxa.

The lack of systematic attention *Acantopsis* has received is especially surprising given their large populations and commercial value in many regions of Southeast Asia. They often are sold in large numbers in markets to be fried and eaten like French fries. Improved taxonomy is a first step toward recognizing isolation vs. interconnectivity among populations and improving management of these fishes and their habitats, but improved ecological information also is sorely needed. It is generally accepted that at least some species migrate (Roberts 1995), but the extent to which migration occurs throughout the genus, as well as the spawning habits, diet, and other life-history characteristics are poorly known for these commercially and environmentally important fishes.

Some species can be difficult to identify, with extreme variation in the color pattern related to habitat conditions at the time of capture or preservation techniques (Fig. 21; Rainboth, *et al*. 2012). However, each species has a unique set of morphological characteristics that remain observable even when the color pattern is obscured, and several species are restricted to single drainages, greatly simplifying identification.

The number of specimens available for analysis of morphological and molecular variation among populations of *Acantopsis* was severely limited for several species, and no molecular data were available for *A. spectabilis* or *A. octoactinotos*. However, material available facilitated the diagnoses of the four previously described species and three newly described species. We are aware of more species to be described, including "*Acantopsis* species" represented in the phylogeny (Fig. 4). We examined few specimens from Borneo, Myanmar, India, Laos, and Cambodia, but predict that more species await description as more material becomes available.

*Acanthopsis lachnostoma* Rutter 1897, described from Swatow, China, has been treated as a species of *Acantopsis* (e.g., Chen 1981, Roberts 1989) or possibly *Cobitis* (Kottelat 2012). As in species of *Acantopsis* the suborbital spine on the holotype (Fig. 22) is anterior to, rather than under, the eye; however, the spine is much closer to the eye than it is in *Acantopsis*, where it is midway between the eye and the tip of the snout. Other characteristics in disagreement with those of *Acantopsis* are the incomplete lateral line, which ends about halfway between the head and the dorsal fin; a crescentic rather than round black spot on the upper base of the caudal fin; and a snout that is not nearly as elongated and pointed as in *Acantopsis*. Also, in the original description, Rutter

(1897) noted the presence of five pairs of barbels, including two on the mandible, which no species of *Acantopsis* is known to have, and a color pattern much more like that of *Cobitis* than of *Acantopsis*: "Body reddish-brown, a series of thirteen dusky spots along lateral line, another of smaller spots along edge of back, a band of small, dusky markings between them; back with dusky blotches, six or seven in median line in front of dorsal." *Acanthopsis lachnostoma* appears to be assignable to *Cobitis;* however, fresh material from the type locality is needed to be certain of the generic assignment.



**FIGURE 21.** Variation in color patterns in preserved specimens of *A. rungthipae*. (A) UF 190191, 77.0 mm SL, 89.4 mm SL, and 90.8 mm SL. (B) UF 190192, 102.7 mm SL.

**FIGURE 22.** *Acanthopsis lachnostoma*, holotype, CAS-SU 1812, 128.1 mm SL. Lateral, ventral, and dorsal views. Image provided by CAS.

## Key to the identification of species of *Acantopsis*

| | | |
|---|---|---|
| 1 | Conspicuous dark spots, blotches, or bands on caudal fin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2 |
| - | No conspicuous dark spots, blotches, or bands on caudal fin . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3 |
| 2 | Large black blotch on tip of anterior rays of dorsal fin; large black blotch on tip of each lobe of caudal fin, smaller black spots or bands in middle of caudal fin; 1 pair of labial barbels . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *A. thiemmedhi* |
| - | No large black blotch on tip of anterior rays of dorsal fin; 2–3 black, irregular bands or blotches on caudal fin, darkest at extremity of lower lobe; 2–3 pairs of labial barbels . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *A. spectabilis* |
| 3 | Well developed ocellus on upper margin of caudal-fin base; 3 pairs of labial barbels . . . . . . . . . . . . . . . . . . . . . . . *A. dialuzona* |
| - | No ocellus on upper margin of caudal-fin base (small black spot may be present); 0–2 pairs of labial barbels . . . . . . . . . . . . 4 |
| 4 | Row of black specks beneath midlateral row of black spots from opercle to pelvic fin. . . . . . . . . . . . . . . . . . . . . . .*A. dinema* |
| - | No row of black specks beneath midlateral row of black spots . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5 |
| 5 | 8½ branched dorsal rays; usually 9 pectoral rays; 2 pairs of labial barbels . . . . . . . . . . . . . . . . . . . . . . . . . . . .*A. octoactinotos* |
| - | 9½ branched dorsal rays, usually 10 pectoral rays; no labial barbels . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 6 |
| 6 | Small black spot on upper margin of caudal-fin base; 9–17 black spots along side of body; 41–43 total vertebrae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . .*A. rungthipae* |
| - | Usually no small black spot on upper margin of caudal-fin base; 13–21 black spots along side of body; 46–48 total vertebrae . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *A. ioa* |

## Literature cited

Abell, R., Thieme, M.L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Contreras Balderas, S., Bussing, W., Stiassny, M.L.J., Skelton, P., Allen, G.R., Unmack, P., Naseka, A., Ng, R., Sindorf, N., Robertson, J., Armijo, E., Higgins, J.V., Heibel, T.J., Wikramanayake, E., Olson, D., López, H.L., Reis, R.E., Lundbert, J.G., Sabaj Pérez, M.H. & Petry, P. (2008) Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *Bioscience*, 58, 403–414.
https://doi.org/10.1641/b580507
Alfred, E.R. (1961a) Notes on a re-examination of some Bleeker type specimens of Indo-Malayan fresh-water fishes. Part 1, Cobitidae and Homalopteridae. *Bulletin of the Raffles Museum*, 30, 32–37.
Alfred, E.R. (1961b) The Javanese fishes described by Kuhl and van Hasselt. *Bulletin of the National Museum of Singapore*, 30, 80–88.
Baldwin, C.C., Mounts, J.H., Smith, D.G. & Weigt, L.A. (2009) Genetic identification and color descriptions of early life-history stages of Belizean *Phaeoptyx* and *Astrapogon* (Teleostei: Apogonidae) with comments on identification of adult *Phaeoptyx*. *Zootaxa*, 2008, 1–22.
Bleeker, P. (1854) Overzigt der ichthyologische fauna van Sumatra, met beschrijving van eenige nieuwe soorten. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, 7, 49–108.
Bleeker, P. (1860) De Visschen van den Indischen Archipel beschreven en toegelicht. Deel 2. Ordo Cyprini, karpers. [Fishes of the Indian Archipelago described and elucidated. Vol. 2. Order Cyprini]. *Acta Societatis Regiae Scientiarum Indo-Neêrlandicae*, 7, i–xiv + 1–492.
Bleeker, P. (1863–64) *Atlas ichthyologique des Indes Orientales Néêrlandaises. Tome III. Cyprins*. Müller, Amsterdam, 150 pp., 43 pls. [pp. 1–48, pls. 102–132 (1863); 49–150, pls. 133–144 (1864).
https://doi.org/10.5962/bhl.title.119362
Bookstein, F., Chernoff, B., Elder, R., Humphries, J., Smith, G. & Strauff, R. (1985) Morphometrics in Evolutionary Biology. *The Academy of Natural Sciences of Philadelphia. Philadelphia, Pennsylvania, Special Publication*, 15, 1–277.
Blyth, E. (1860) Report on some fishes received chiefly from the Sitang river and its tributary streams, Tenasserim Provinces. *Journal of the Asiatic Society of Bengal*, 29, 138–174.
Chakrabarty, P., Warren, M., Page, L. & Baldwin, C. (2013) GenSeq: An updated nomenclature for genetic sequences and a formal ranking of sequences from type and non-type sources. *ZooKeys*, 346, 29–41.
https://doi.org/10.3897/zookeys.346.5753
Chen, J.-X. (1981) A study on the classification of the subfamily Cobitinae in China. *Transactions of the Chinese Ichthyological Society*, 1, 21–31. [in Chinese]
Cuvier, G. & Valenciennes, A. (1846) *Histoire naturelle des Poisson. Tome dix-huitième.* Bertrand, Paris, xix + 505 pp.
https://doi.org/10.5962/bhl.title.7339
Eschmeyer, W.N., Fricke, R. & van der Laan, R. (Eds.) (2016) Catalog of Fishes: Genera, species, references. Electronic version. Available from: http://researcharchive.calacademy.org/research/ ichthyology/catalog/fishcatmain.asp (accessed 31 December 2016)
Fricke, R. & Eschmeyer, W.N. (2016) A guide to the fish collections in the Catalog of Fishes. Electronic version. Available from: http://researcharchive.calacademy.org/research/ichthyology/ catalog/fishcatmain.asp (accessed 11 December 2016)
Havird, J.C., Page, L.M., Tangjitjaroen, W., Vidthayanon, C., Grudpan, C. & Udduang, S. (2010) A new species of *Lepidocephalichthys* (Teleostei: Cobitidae) with distinctive sexual dimorphism and comments on relationships in southern

lineages of Cobitidae. *Zootaxa*, 2557, 1–18.

Hubbs, C.L., Lagler, K.F. & Smith, G.R. (2004) *Fishes of the Great Lakes Region*. University of Michigan, Ann Arbor, 276 pp., 32 pls.
https://doi.org/10.3998/mpub.17658

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17, 754–755.
https://doi.org/10.1093/bioinformatics/17.8.754

Humphries, J.M., Bookstein, F.L., Chernoff, B., Smith, G.R., Elder, R.L. & Poss, S.G. (1981) Multivariate discrimination by shape in relation to size. *Systematic Zoology*, 30, 291–308.
https://doi.org/10.2307/2413251

Inger, R.F. & Chin, P.K. (1962) The fresh-water fishes of North Borneo. *Fieldiana, Zoology*, 45, 1–268.
https://doi.org/10.5962/bhl.title.2957

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. & Drummond, A. (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28, 1647–1649.
https://doi.org/10.1093/bioinformatics/bts199

Kottelat, M. (1987) Nomenclatural status of the fish names created by J. C.van Hasselt (1823) and of some cobitoid genera. *Japanese Journal of Ichthyology*, 33, 368–375.

Kottelat, M. (1990) *Indochinese nemacheilines. A revision of nemacheiline loaches (Pisces: Cypriniformes) of Thailand, Burma, Laos, Cambodia and southern Viet Nam*. Pfeil, München, 262 pp.

Kottelat, M. (2012) Conspectus cobitidum: an inventory of the loaches of the world (Teleostei: Cypriniformes: Cobitoidei). *Raffles Bulletin of Zoology Supplement*, 26, 1–199.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: Combined Selection of Partitioning Schemes and Substitution Models for Phylogenetic Analyses. *Molecular Biology and Evolution*, 29, 1695–1701.
https://doi.org/10.1093/molbev/mss020

Larkin, M.A., Blackshields, G., Brown, N.P., Chenna, R., McGettigan, P. A., McWilliam, H., Valentin, F., Wallace, I.M., Wilm, A., Lopez, R., Thompson, J.D., Gibson, T.J. & Higgins, D.G. (2007) Clustal W and Clustal X version 2.0. *Bioinformatics*, 23, 2947–2948.
https://doi.org/10.1093/bioinformatics/btm404

Liu, S.Q., Mayden, R.L., Zhang, J.B., Yu, D., Tang, Q.Y., Deng, X. & Liu, H.Z. (2012) Phylogenetic relationships of the Cobitoidea (Teleostei: Cypriniformes) inferred from mitochondrial and nuclear genes with analyses of gene evolution. *Gene*, 508, 60–72.
https://doi.org/10.1016/j.gene.2012.07.040

Maddison, W. P. & Maddison, D. R. (2016) *Mesquite: a modular system for evolutionary analysis. Version. 3.11*. Available from: http://mesquiteproject.org (accessed 14 August 2017)

Martin-Smith, K.M. & Hui, T.H. (1998) Diversity of freshwater fishes from eastern Sabah: annotated checklist for Danum Valley and a consideration of inter- and intra-catchment variability. *Raffles Bulletin of Zoology*, 46, 573–604.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *In: Gateway Computing Environments Workshop (GCE)*, *2010*. IEEE, pp. 1–8.
https://doi.org/10.1109/gce.2010.5676129

Page. L.M. & Tangjitjaroen, W. (2015) *Aperioptus pictorius* Richardson 1848 is a senior synonym of *Acanthopsoides molobrion* Siebert 1991, and *Aperioptus* is a senior synonym of *Acanthopsoides* Fowler 1934 (Cypriniformes: Cobitidae). *Zootaxa*, 3962 (1), 179–181.
https://doi.org/10.11646/zootaxa.3962.1.10

Rainboth, W.J., Vidthayanon, C. & Mai, D.Y. (2012) Fishes of the greater Mekong ecosystem with species list and photographic atlas. *Miscellaneous Publications*, *Museum of Zoology, University of Michigan*, 21, 1–173, 121 pls.

Randall, Z.S. & Page, L.M. (2015) On the paraphyly of *Homaloptera* (Teleostei: Balitoridae) and description of a new genus of hillstream loaches from the Western Ghats of India. *Zootaxa*, 3926 (1), 57–86.
https://doi.org/10.11646/zootaxa.3926.1.2

Randall, Z.S. & Riggs, P.A. (2015) Revision of the hillstream lizard loaches, genus *Balitoropsis* (Cypriniformes: Balitoridae). *Zootaxa*, 3962, 206–225.
https://doi.org/10.11646/zootaxa.3962.1.13

Roberts, T.R. (1989) The freshwater fishes of western Borneo (Kalimantan Barat, Indonesia). *Memoirs of the California Academy of Sciences*, 14, 1–210.
https://doi.org/10.2307/1446567

Roberts, T.R. (1993) The freshwater fishes of Java, as observed by Kuhl and van Hasselt in 1820–1823. *Zoologische Verhandelingen*, 285, 1–94.

Roberts, T.R. (1995) Traditional fisheries and fish ecology on the Mekong River at Rhone Waterfalls in southern Laos. *Natural History Bulletin of the Siam Society*, 43, 219–262.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suichard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.

https://doi.org/10.1093/sysbio/sys029

Rutter, C. (1897) A collection of fishes obtained in Swatow, China, by Miss Adele M. Fielde. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1897, 56–90.

Rüppell, E. (1852) *Verzeichniss der in dem Museum der Senckenbergischen naturforschenden Gesellschaft aufgestellten Sammlungen*. Vierte Abtheilung. Fische und deren Skelette. Senckenbergische Naturforschenden Gesellschaft, Frankfurt, iv+40 pp.

Siebert, D.J. (1991a) Revision of *Acanthopsoides* Fowler, 1934 (Cypriniformes: Cobitidae), with the description of new species. *Japanese Journal of Ichthyology*, 38, 97–114.
http://doi.org/10.11369/jji1950.38.97

Siebert, D.J. (1991b) *Acantopsis octoactinotos*, a new species of horse-faced loach (Cypriniformes: Cobitidae) from Sabah, Malaysia. *Copeia*, 1991, 910–915.
https://doi.org/10.2307/1446086

Silvestro, D. & Michalak, I. (2012) raxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution*, 12, 335–337.
https://doi.org/10.1007/s13127-011-0056-0

Šlechtová, V., Bohlen, J. & Tan, H.H. (2007) Families of Cobitoidea (Teleostei; Cypriniformes) as revealed from nuclear genetic data and the position of the mysterious genera *Barbucca*, *Psilorhynchus*, *Serpenticobitis* and *Vaillantella*. *Molecular Phylogenetics and Evolution*, 44, 1358–1365.
https://doi.org/10.1016/j.ympev.2007.02.019

Šlechtová, V., Bohlen, J. & Perdices, A. (2008) Molecular phylogeny of the freshwater fish family Cobitidae (Cypriniformes: Teleostei): Delimitation of genera, mitochondrial introgression and evolution of sexual dimorphism. *Molecular Phylogenetics and Evolution*, 47, 812–831.
https://doi.org/10.1016/j.ympev.2007.12.018

Sontirat, S. (1999) Description of a new species of *Acantopsis* (Cypriniformes: Cobitidae) from Thailand. *In*: Seret, B. & Sire, J.-Y. (Eds.), *Proceedings of the 5th Indo-Pacific Conference*, *Nouméa*, *1997*. Société Française d'Ichtyologie, Paris, pp. 65-68.

Tamura, K., Dudley, J., Nei, M. & Kumar, S. (2007) MEGA4: molecular evolutionary genetics analysis (MEGA) software version 4.0. *Molecular Biology and Evolution*, 24, 1596–1599.
https://doi.org/10.1093/molbev/msm092

van Hasselt, J.C. (1823) Extract from a letter from Dr. J. C. van Hasselt to Mr. C. J. Temminck, written from Tjecande, Residency of Bantam, on 29th December, 1822. [Uittreksel uit een' brief van den Heer J. C. van Hasselt, aan den Heer C. J. Temminck, geschreven uit Tjecande, Residentie Bantam, den 29sten December 1822.] *Algemeene Konst-en Letter-Bode voor het Jaar 1823*, *II Deel*, 35, 130–133.
https://doi.org/10.1163/2214-8264_dutchpamphlets-kb2-kb27429

van Hasselt, J.C. (1824) Extrait d'une seconde lettre sur les poissons de Java, écrite par M. van Hasselt à M. C.-J. Temminck, datée de Tjecande, résidence de Bantam, 29 décembre 1822. *Bulletin Universel des Sciences et de l'Industrie*, *Section 2*, *Bulletin des Sciences Naturelles et de Géologie*, 2, 374–377.

van Oijen, M.J.P. & Loots, G.M.P. (2012) An illustrated translation of Bleeker's Fishes of the Indian Archipelago. Part II. Cyprini. *Zoologische Mededelingen*, 86, 1–469.

Vishwanath, W. & Laisram, J. (2005) A new fish of the genus Acantopsis van Hasselt (Cypriniformes: Cobitidae) from Manipur, Indin [India]. *Journal of the Bombay Natural History Society*, 101, 433–436.

**APPENDIX A.** Material Examined. Numbers of specimens on which counts and measurements were made are in bold. Primary and secondary types of species described herein are excluded.

*Acantopsis dialuzona*—**Thailand**: ANSP 76846, 1, Kachong River, trib. of Trang River, at waterfall in Chong, 7.549N, 99.784E; CAS 238297, 8, Sai Buri River at Raman, 6.475N, 101.443E. **Malaysia:** UF 235413, 2, Padang Terap River off K11 at Padang Sanai, 6.342N, 100.688E; UF 235417, 2, Jedok River, trib. of Golok River, off FT196, 5.836N, 101.960E; UF 236150, 14, Jedok River, trib. of Golok River, off RT199, 4 km S of Kelisar, 5.751N, 101.981E; UF 235414, 3, Besut River 3.5 km SSW of Jerteh, 5.709N, 102.480E; UF 235416, 3, Pur River, trib. of Terengganu River, 7.5 km SW of Kuala Berang, 5.025N, 102.968E; UF 235415, 3, Terengganu River at Kenyir Dam, 5.024N, 102.908E; UF 173552, **5** of **8**, trib. of Sedili Besar River off FT3, 30 km S of Jemaluang, 2.115N, 103.869E; UF 173516, 4, Sayong River, trib. of Johor River, on J25, N of Layang-Layang, 1.848N, 103.483E; UF 173514, 2, trib. of Sayong River on J25, S of Layang-Layang, 1.800N, 103.500E. **Indonesia:** USNM 230260, 1, Kapuas River 6 km W of Putussibau, 0.842N, 112.867E; CAS 238324, 1, Belayan River 8–9 km upstream from Tabang, 0.586N, 115.973E; CAS 238558, **3**, Rawas River, trib. of Musi River, near Muara Rupit and Surulangun, 2.663S, 102.832E; UF 166886, **2**, Lekukam Creek, trib. of Lematang River, 25 km NNE of Muara Enim, 3.460S, 103.893E; UF 166890, **10** of **11**, Rambang River, trib. of Ogan River, 11 km S of Prabumulih, 3.550S, 104.264E; RMNH 4977, 1 (lectotype of *Cobitis choirorhynchos*), confluence of Lematang and Enim Rivers, 3.650S, 103.770E; UF 166888, 1, Ogan River, trib. of Musi River, 3.5 km NW of Baturaja, 4.106S, 104.138E; UF 166895, 1, Sungkai River at confluence with Kanan River, 4.605S, 104.964E; UF 161621, **3** of **5**, Pegadungan River W of Way Kambas National Park, 4.884S, 105.579E; UF 161717, 9, Gedongwani River, trib. of Sekampung River, 5.242S, 105.484E; RMNH 2707, 1 (syntype), Batavia, present-day Jakarta.

*Acantopsis spectabilis*—**Myanmar:** THNHM F0013597, 1, trib. of Chindwin River 32.5 km SSW of Khamti, 25.742N, 95.542E; CAS 88783, **4**, Mali River upstream of confluence with N'Mai River, 25.711N, 97.506E; USNM 372415, 4, same as CAS 88783; UF 190927, 1, Nam Saing River, trib. of Chindwin River, 25.512N, 95.444E; THNHM F0013596, **1** of **3**, Nampagan Creek at confluence with Chindwin River, 25.389N, 95.377E; USNM 372473, 3, Irrawaddy River S of Myitkyina, 25.336N, 97.382E; CAS 231715, 2, Irrawaddy River at Sinywa, 1 km S of Mingun, 22.022N, 96.032E; CAS 231480, 16, Irrawaddy River 10 km W of Ngazun, 21.913N, 95.584E; CAS 231348, 2, Irrawaddy River NE of confluence with Chindwin River, 21.482N, 95.305E; CAS 231172, 1, Irrawaddy River 0.7 km N of Nyaung Oo, 21.206N, 94.906E; RLIKU 1920, **4** of **7**, trib. of Dawei River at Pagagyi, 14.104N, 98.305E. **Thailand:** CAS 238307, **1**, Moei River on Rt. 1085, 129 km N of Mae Sot, 17.514N, 97.968E; CAS 238298, **1**, Moei River on Rt. 1085, 121 km N of Mae Sot, 17.467N, 98.026E; NIFI 2456, 5, Mae Lamao River, trib. of Moei River, in Mae Sot, 16.836N, 98.592E; CAS 238563, **2** of **3**, Moei River.

*Acantopsis octoactinotos*—**Malaysia**: FMNH 68146, **6** of **15**, trib. of Kinabatangan River near Deramakot River, 5.291N, 117.552E; FMNH 68150, 10, trib. of Kinabatangan River near Deramakot River, 5.289N, 117.550E; FMNH 68145, 7, trib. of Kinabatangan River near Deramakot River, 5.284N, 117.548E; FMNH 68148, 1 (holotype), trib. of Kinabatangan River near Deramakot River, 5.276N, 117.544E; FMNH 68147, 5, trib. of Kinabatangan River near Deramakot River, 5.273N, 117.540E.

*Acantopsis thiemmedhi*—**Thailand:** NIFI 2974, **2** of **3**, Mae Pam River, trib. of Ping River, in Chiang Dao, 19.457N, 99.044E; CAS 238314, 1, Wang River 1.5 km NW of Chae Khon, 18.932N, 99.649E; CAS 238564, 7, same as CAS 238314; CAS 243718, 1, same as CAS 238314; NIFI 4376, **1**, Mae Kuam River off Rt. 1157 at Pang Da, 18.688N, 99.487E; UF 187664, **6** of **10**, Wang River downstream of Kiew Lom Dam, 18.519N, 99.633E; UF 188120, 2, Wang River, Lampang Inland Fisheries Research and Development Center, 18.417N, 99.544E; UF 188118, **1** of **2**, Mae Tui River, trib. of Wang River, NE of Khae, 18.379N, 99.444E; KUMF 3132, **6** of **16**, Mae Phrik Creek at Mae Phrik, 17.448N, 99.120E; KUMF 3131, **1** (holotype), Nam Khun Creek at Huai Kha Khaeng Wildlife Sanctuary, 15.610N, 99.312E; CAS 243716, **2**, Thap Salao River at Huai Kha Khaeng Wildlife Sanctuary, 15.608N, 99.319E; KUMF 3133, **2**, same as CAS 243716; KUMF 3134, 2, Chao Phraya River at Tha Nam Oi, 15.427N, 100.135E.

*Acantopsis rungthipae*—**Thailand:** CAS 238306, 2, Kok River at Tha Ton, 20.039N, 99.477E; USNM 229326, 3, same as CAS 238306; USNM 229327, 1, Fang River, trib. of Kok River, on Rt. 107, 34 km S of Fang, 19.637N, 99.130E; CAS 238322, 1, Ping River 15 km N of Chiang Mai, 18.941N, 98.976E; CAS 238296, 101, Wang River 1.5 km NW of Chae Khon, 18.932N, 99.649E; CAS 238318, 58, same as CAS 238296; CAS 238559, 9, same as CAS 238296; CAS 238565, 51, same as CAS 238296; UF 188117, **2**, same as CAS 238296; UF 181092, 2, Wang River on Rt 1335, 2 km E of Chae Hom, 18.706N, 99.588E; UF 187665, 13, Wang River downstream of Kiew Lom Dam, 18.519N, 99.633E; UF 188211, 8, Yom River, trib. of Nan River, downstream of dam at Nun Nuea, 18.484N, 100.158E; UF 188121, 58, Wang River, Lampang Inland Fisheries Research and Development Center, 18.417N, 99.544E; CAS 238309, **4** of **6**, Mae Chaem River on Rt. 108, 10-16 km W of Hot, 18.230N, 98.518E; CAS 238320, **3**, Hueang Creek on Rt. 2195, 22 km W of Chiang Khan, 17.794N, 101.573E; UF 188115, **12** of **29**, Songkhram River at mouth of Yam River, 17.709N, 104.077E; UF 188114, **2**, Songkhram River at mouth of Nam Mao River, 17.702N, 104.256E; CAS 238312, 64, Songkhram River on Rt. 2390 at Hat Phaeng, 17.674N, 104.285E; CAS 238323, 3, same as CAS 238312; CAS 238308, 21, Mekong River near mouth of Songkhram River, 17.653N, 104.466E; UF 188213, 24, Un River, trib. of Songkhram River, on Rt. 4029, 3 km E of Na Wa, 17.480N, 104.129E; UF 188119, **2** of **3**, Wang River on Rt. 1102, E of Mae Phrik, 17.446N, 99.129E; UF 188122, 11, Phak River, trib. of Khwae Noi River, on Rt. 1143 at Tha Sakae, 17.253N, 100.629E; UMMZ 236745, **6** of **14**, Ping River downstream of Bhumibol Dam, 17.242N, 99.000E; UF 188125, 2, Yom River on Rt. 1293 at Yang Sai, 16.980N, 99.832E;

CAS 238304, 24, Ngaem River S of That Phanom, 16.866N, 104.746E; CAS 219362, 4, Phong River, trib. of Chi River, at Nam Phong, 16.704N, 102.842E; UF 188223, 1, Thom Creek on Rt. 2034, S of Hin Khan, 16.122N, 105.031E; UF 188124, **3** of **4**, Ta Wang River on Rt. 2112, 4 km S of Rt. 2337, 15.792N, 105.376E; UF 188224, 1, same as UF 188124; UF 172928, 1, Sa Thung River at Samrong, 15.744N, 105.460E; CAS 238562, **1** of **11**, Thap Salao River at Huai Kha Khaeng Wildlife Sanctuary, 15.608N, 99.319E; ANSP 178820, 1, Chao Phraya at Phayuha Khiri, 15.454N, 100.134E; AUM 55879, **6**, Mekong River 2.4 km E of Khong Chiam, 15.321N, 105.515E; UF 188112, 4, Mun River opposite Krasang, 15.315N, 103.630E; UMMZ 224554, **1**, Hin Taek Creek 1.5 km from confluence with Mun River, 15.298N, 105.495E; UMMZ 195732, **1**, Mun River 20 km downstream of Ubon Ratchathani, 15.285N, 105.061E; USNM 305221, 2, Mun River downstream of dam at Phimai, 15.234N, 102.508E; UMMZ 195716, **1**, Mun River 5 km downstream of Ubon Ratchathani, 15.233N, 104.934E; UMMZ 233877, 14, Mun River 3 km downstream of Ubon Ratchathani, 15.228N, 104.926E; AUM 56000, **5** of **42**, Chi River 2 km upstream of confluence with Mun River, 15.195N, 104.713E; AUM 56001, 2, same as AUM 56000; AUM 56002, 1, same as AUM 56000; AUM 55977, 1, Mun River at mouth of Chi River, 15.182N, 104.714E; UF 188109, 14, same as AUM 55977; CAS 238317, 1, Lam Kha Khaeng River at mouth of Krueng Krai Creek, 15.025N, 99.188E; UF 190875, 6, Taphoen River off Rt. 3086, 7 km NNW of Nong Prue, 14.666N, 99.444E; UF 190874, 5, Taphoen River on Rt. 3086 at Lum Rang, 14.430N, 99.503E; UF 188123, 2, Taphoen River, trib. of Khwae Yai River, at Thung Masang, 14.200N, 99.484E; CAS 238556, 13, Khamong River, trib. of Bang Pakong River, on Rt. 304, 14.046N, 101.790E; UMMZ 195851, 2, Mae Khlong River at Kanchanaburi, 14.019N, 99.527E; UMMZ 236724, 3, Khwae Noi River 4 km upstream of Kanchanaburi, 13.992N, 99.509E; UMMZ 195821, 1, Khwae Noi River 18 km upstream of Kanchanaburi, 13.930N, 99.499E; UMMZ 195837, 1, Khwae Noi River 20 km upstream of Kanchanaburi, 13.923N, 99.477E; CAS 238299, 9, Phra Sathueng River, trib. of Bang Pakong River, at Khao Chakan, 13.668N, 102.076E; ANSP 87275, 4, Tha Chin River at Tha Chin, 13.544N, 100.250E; USNM 103299, 6, Mae Khlong River at Ratchaburi, 13.542N, 99.819E; CAS 238321, 1, Won Creek, trib. of Tapi River, on Rt. 4009, 8.582N, 99.281E; CAS 238313, 19, Ipan River, trib. of Tapi River, on Rt. 4037, 8.548N, 99.110E; UF 236085, 2, Tapi River on Rt. 4015, 5 km NNE of Than Pho, 8.507N, 99.509E. **Laos:** UMMZ 240683, **6** of **8**, Nam Lik River 6 km upstream of confluence with Nam Ngum River, 18.581N, 102.504E; UMMZ 241649, 1, Nam Ngang upstream of confluence with Nam Leuk, 18.368N, 103.091E; UMMZ 250310, **1**, Xe Bangfai River opposite Hatkhamhiang, 17.067N, 104.905E; UMMZ 241863, 2, Mekong River at Salao, 15.074N, 105.825E; CAS 238293, 2, market at Attapeu, 14.801N, 106.836E. **Cambodia:** UF 190189, 4, Kong River 10 km upstream of confluence with Srepok River, 13.610N, 106.092E; UF 190187, 3, Mekong River at mouth of Sekong River, 13.532N, 105.947E; UF 190193, 36, Pursat River 14 km NE of Pursat, 12.624N, 104.009E; UMMZ 246578, 2, Pursat River 12 km WSW of Pursat, 12.501N, 103.831E; UF 190191, 19, Prek Te River on NR7, 12.393N, 106.241E; UF 190192, 15, Baribo River, trib. of Tonle Sap, 9 km SSW of Phsar, 12.357N, 104.409E; UMMZ 246543, 1, Pursat River 8 km NE of Pramaoy, 12.344N, 103.163E; UMMZ 246519, 1, trib. of Pursat River at Anlong Reap, 12.279N, 103.013E; UMMZ 235726, 1, Tonle Sap 35.5 km upsteam of Phnom Penh, 11.733N, 104.833E; UMMZ 234757, 8, Mekong River N of Koh Dach Island, 11.709N, 104.963E; CAS 238294, 25, Tonle Sap 13-16 km N of Phnom Penh, 11.686N, 104.848E; UMMZ 246585, 6, Prek Thnot River S of NR44 and NR132 intersection, 11.674N, 104.124E; UMMZ 250309, 4, Prek Thnot River at Kampong Speu, 11.460N, 104.521E. **Vietnam:** UMMZ 224817, 67, Bassac River S of Vinh Truong Island, 10.746N, 105.134E.

*Acantopsis dinema*—**Thailand:** UF 188219, 4, Songkhram River 1.5 km W of Na Si Nuan, 17.729N, 103.411E; UF 188215, 1, Thuai River on Rt. 212, S of Tha Uthen, 17.562N, 104.609E; UF 188212, 4, Un River, trib. of Songkhram River, on Rt. 4029, 3 km E of Na Wa, 17.480N, 104.129E; UF 188216, 1, Kong Si Creek off Rt. 2025, E of Tum Tai, 17.097N, 102.989E; UMMZ 209445, 1, Ubolratana Reservoir, 16.762N, 102.587E; UMMZ 195630, 3, Mekong River at Mukdahan, 16.547N, 104.734E; UF 188113, 3, Pao River, trib. of Chi River, on Rt. 214, 16.340N, 103.576E; ANSP 87235, 2, Mekong River at Khemmarat, 16.044N, 105.224E; UF 188111, 3, Mun River opposite Krasang, 15.315N, 103.630E; UMMZ 195716, **4**, Mun River 5 km downstream of Ubon Ratchathani, 15.233N, 104.934E; UMMZ 217613, **1**, Mun River 1.3 km upstream of Ubon Ratchathani, 15.229N, 104.858E; UMMZ 250308, 7, Mun River 3 km downstream of Ubon Ratchathani, 15.228N, 104.926E; AUM 55999, 4, Chi River 2 km upstream of confluence with Mun River, 15.195N, 104.713E; AUM 56003, 3, same as AUM 55999; AUM 55976, 4, Mun River at mouth of Chi River, 15.182N, 104.714E; UF 188110, 1, same as AUM 55976; AUM 55956, 3, trib. of Tong Waet River 7.3 km SSE of Warin Chamrap, 15.130N, 104.888E; THNHM F0000058, 1, Plai Mat River, trib. of Mun River, at Nong Sai, 14.692N, 102.743E; THNHM F0001177, 1, Chiang Sa River, trib. of Mun River, at Nong Samong, 14.508N, 101.966E; THNHM F0005213, 1, same as THNHM F0001177; THNHM F0005214, 1, same as THNHM F0001177. **Laos:** UMMZ 241591, **5** of **6**, Xe Bangfai River opposite Hatkhamhiang, 17.067N, 104.905E. **Cambodia:** THNHM F0013593, 1, Stung Sreng River upstream from Kralanh, 13.613N, 103.408E; UF 190864, 6, Pursat River 14 km NE of Pursat, 12.624N, 104.009E; UMMZ 234520, 4, Prek Thnot River at Kampong Speu, 11.460N, 104.521E.

*Acantopsis ioa*—**Thailand:** UF 188214, 37, Mekong River at Bung Khla, 38 km E of Bueng Kan, 18.301N, 103.998E; CAS 238561, 34, Mekong River 90 km NE of Chiang Khan, 18.211N, 102.102E; CAS 238311, 37, Mekong River on Rt. 211 at Hat Bia, 18.058N, 101.804E; CAS 63027, 85, Mekong River at Chiang Khan, 17.895N, 101.652E; CAS 238310, 2, same as CAS 63027; UMMZ 195472, 25, Mekong River 10 km upstream of Nong Khai, 17.818N, 102.700E; CAS 238319, 1, Mekong River 12 km S of That Phanom, 16.848N, 104.759E; UF 188134, 32, Mekong River at Song Khon, 25.5 km N of Mukdahan, 16.775N, 104.740E; UF 188136, 25, same as UF 188134; UMMZ 250306, 1, Mekong River at Mukdahan, 16.547N, 104.734E; UF 188133, 50, Mekong River at mouth of Mun River, 15.318N, 105.513E. **Laos:** UMMZ 240658, **1**, Nam Xuang River at Pakxuang, 19.972N, 102.243E; UMMZ 241864, 17, Mekong River at Salao, 15.074N, 105.825E. **Cambodia:** UF 190190, 1, Srepok River 40 km E of Stung Treng, 13.501N, 106.354E.

*Acantopsis* **species—Thailand:** UMMZ 250307, 1, Mae Khlong River at Kanchanaburi, 14.019N, 99.527E; UF 235990, 5, Phachi River, trib. of Khwae Noi River, on Rt. 3085, 13.918N, 99.382E. **Cambodia:** UF 190188, 19, Kong River 10 km upstream of confluence with Srepok River, 13.610N, 106.092E.

*Acanthopsis lachnostoma*—**China:** CAS-SU 1812, 1 (holotype), Guangdon, Shantou (Swatow), 23.343N, 116.708E.

**APPENDIX B.** Specimens of *Acantopsis* included in the molecular phylogeny and their associated catalog, tissue, and Genbank accession numbers, and GenSeq designations. Sampling locations are available in Appendix A and at http://specifyportal.flmnh.ufl.edu/fishes and iDigBio.org. GenSeq designations follow Chakrabarty *et al*. (2013).

| Species | Catalog Number | Tissue Number | COI | RAGI | GenSeq |
|---|---|---|---|---|---|
| *A. dialuzona* | UF 161621 | 2005-0882 | MF509900 | MF510011 | genseq-3 |
| | | 2005-0883 | MF509901 | MF510012 | genseq-3 |
| | UF 161717 | 2005-1006 | MF509902 | MF510013 | genseq-3 |
| | | 2005-1007 | MF509903 | MF510014 | genseq-3 |
| | UF 166890 | 2006-0666 | MF509904 | MF510015 | genseq-3 |
| | UF 173514 | 2008-0635 | MF509906 | MF510017 | genseq-3 |
| | UF 173516 | 2008-0640 | MF509907 | MF510018 | genseq-3 |
| | | 2008-0641 | MF509908 | MF510019 | genseq-3 |
| | UF 173552 | 2008-0692 | MF509909 | MF510020 | genseq-3 |
| | | 2008-0693 | MF509910 | MF510021 | genseq-3 |
| | | 2008-0696 | MF509911 | MF510022 | genseq-3 |
| | | 2008-0698 | MF509912 | MF510023 | genseq-3 |
| | UF 236150 | 2012-0576 | MF509923 | MF510034 | genseq-3 |
| | | 2012-0594 | MF509924 | MF510035 | genseq-3 |
| | | 2012-0604 | MF509925 | MF510036 | genseq-3 |
| | | 2012-0606 | MF509926 | MF510037 | genseq-3 |
| *A. thiemmedhi* | UF 187664 | 2012-0545 | MF509919 | MF510030 | genseq-3 |
| | | 2012-0546 | MF509920 | MF510031 | genseq-3 |
| | | 2012-0547 | MF509921 | MF510032 | genseq-3 |
| | | 2012-0548 | MF509922 | MF510033 | genseq-3 |
| | UF 188118 | 2015-0163 | MF509951 | MF510062 | genseq-3 |
| | | 2015-0174 | MF509952 | MF510063 | genseq-3 |
| | UF 188120 | 2015-0189 | MF509958 | MF510069 | genseq-3 |
| *A. rungthipae* | THNHM F0013610 | 2014-0149 | MF509927 | MF510038 | genseq-1 |
| | UF 235976 | 2014-0152 | MF509928 | MF510039 | genseq-2 |
| | | 2014-0154 | MF509929 | MF510040 | genseq-2 |
| | ZRC 55596 | 2014-0169 | MF509930 | MF510041 | genseq-2 |
| | UF 172928 | 2008-0530 | MF509905 | MF510016 | genseq-3 |
| | UF 181092 | 2011-0264 | MF509913 | MF510024 | genseq-3 |
| | | 2011-0266 | MF509914 | MF510025 | genseq-3 |
| | UF 187665 | 2012-0541 | MF509915 | MF510026 | genseq-3 |
| | | 2012-0542 | MF509916 | MF510027 | genseq-3 |
| | | 2012-0543 | MF509917 | MF510028 | genseq-3 |
| | | 2012-0544 | MF509918 | MF510029 | genseq-3 |
| | UF 188109 | 2015-0001 | MF509936 | MF510047 | genseq-3 |

| Species | Catalog Number | Tissue Number | COI | RAGI | GenSeq |
|---------|----------------|---------------|-----|------|--------|
| *A. rungthipae* | | 2015-0002 | MF509937 | MF510048 | genseq-3 |
| | | 2015-0003 | MF509938 | MF510049 | genseq-3 |
| | UF 188112 | 2015-0009 | MF509940 | MF510051 | genseq-3 |
| | UF 188114 | 2015-0060 | MF509942 | MF510053 | genseq-3 |
| | | 2015-0065 | MF509943 | MF510054 | genseq-3 |
| | UF 188115 | 2015-0077 | MF509944 | MF510055 | genseq-3 |
| | UF 188117 | 2015-0160 | MF509949 | MF510060 | genseq-3 |
| | | 2015-0161 | MF509950 | MF510061 | genseq-3 |
| | UF 188119 | 2015-0176 | MF509953 | MF510064 | genseq-3 |
| | | 2015-0183 | MF509954 | MF510065 | genseq-3 |
| | | 2015-0185 | MF509955 | MF510066 | genseq-3 |
| | UF 188121 | 2015-0187 | MF509956 | MF510067 | genseq-3 |
| | | 2015-0188 | MF509957 | MF510068 | genseq-3 |
| | | 2015-0190 | MF509959 | MF510070 | genseq-3 |
| | UF 188122 | 2015-0194 | MF509960 | MF510071 | genseq-3 |
| | | 2015-0197 | MF509961 | MF510072 | genseq-3 |
| | | 2015-0198 | MF509962 | MF510073 | genseq-3 |
| | UF 188123 | 2015-0371 | MF509963 | MF510074 | genseq-3 |
| | | 2015-0378 | MF509964 | MF510075 | genseq-3 |
| | UF 188211 | ICH-00105 | MF509973 | MF510084 | genseq-3 |
| | | ICH-00107 | MF509974 | MF510085 | genseq-3 |
| | UF 188213 | ICH-00233 | MF509981 | MF510092 | genseq-3 |
| | | ICH-00240 | MF509983 | MF510094 | genseq-3 |
| | UF 188223 | ICH-00906 | MF509988 | MF510099 | genseq-3 |
| | UF 188224 | ICH-00963 | MF509991 | MF510102 | genseq-3 |
| | UF 190187 | ICH-01215 | MF509993 | MF510104 | genseq-3 |
| | | ICH-01216 | MF509994 | MF510105 | genseq-3 |
| | | ICH-01217 | MF509995 | MF510106 | genseq-3 |
| | UF 190189 | ICH-01268 | MF509999 | MF510110 | genseq-3 |
| | UF 190191 | ICH-01330 | MF510001 | MF510112 | genseq-3 |
| | | ICH-01334 | MF510002 | MF510113 | genseq-3 |
| | | ICH-01335 | MF510003 | MF510114 | genseq-3 |
| | | ICH-01336 | MF510004 | MF510115 | genseq-3 |
| | | ICH-01339 | MF510005 | MF510116 | genseq-3 |
| | UF 190192 | ICH-01359 | MF510006 | MF510117 | genseq-3 |
| | | ICH-01366 | MF510007 | MF510118 | genseq-3 |
| | | ICH-01372 | MF510008 | MF510119 | genseq-3 |
| | | ICH-01380 | MF510009 | MF510120 | genseq-3 |
| | UF 190193 | ICH-01386 | MF510010 | MF510121 | genseq-3 |
| | UF 236085 | 2014-0258 | MF509931 | MF510042 | genseq-3 |
| | | 2014-0261 | MF509932 | MF510043 | genseq-3 |

| Species | Catalog Number | Tissue Number | COI | RAGI | GenSeq |
|---|---|---|---|---|---|
| *A. dinema* | THNHM F0013611 | ICH-00956 | MF509989 | MF510100 | genseq-1 |
| | UF 188225 | ICH-00957 | MF509990 | MF510101 | genseq-2 |
| | | ICH-00964 | MF509992 | MF510103 | genseq-2 |
| | UF 188116 | 2015-0078 | MF509945 | MF510056 | genseq-2 |
| | | 2015-0079 | MF509946 | MF510057 | genseq-2 |
| | | 2015-0080 | MF509947 | MF510058 | genseq-2 |
| | | 2015-0081 | MF509948 | MF510059 | genseq-2 |
| | UF 188111 | 2015-0006 | MF509939 | MF510050 | genseq-3 |
| | UF 188113 | 2015-0028 | MF509941 | MF510052 | genseq-3 |
| | UF 188212 | ICH-00232 | MF509980 | MF510091 | genseq-3 |
| | | ICH-00234 | MF509982 | MF510093 | genseq-3 |
| | UF 188215 | ICH-00262 | MF509987 | MF510098 | genseq-3 |
| | UF 188216 | ICH-00140 | MF509975 | MF510086 | genseq-3 |
| | UF 188219 | ICH-00195 | MF509976 | MF510087 | genseq-3 |
| | | ICH-00198 | MF509977 | MF510088 | genseq-3 |
| | | ICH-00199 | MF509978 | MF510089 | genseq-3 |
| | | ICH-00201 | MF509979 | MF510090 | genseq-3 |
| *A. ioa* | UF 188135 | 2015-0491 | MF509965 | MF510076 | genseq-2 |
| | | 2015-0492 | MF509966 | MF510077 | genseq-2 |
| | | 2015-0493 | MF509967 | MF510078 | genseq-2 |
| | | 2015-0494 | MF509968 | MF510079 | genseq-2 |
| | UF 188136 | 2015-0495 | MF509969 | MF510080 | genseq-3 |
| | | 2015-0496 | MF509970 | MF510081 | genseq-3 |
| | | 2015-0497 | MF509971 | MF510082 | genseq-3 |
| | | 2015-0498 | MF509972 | MF510083 | genseq-3 |
| | UF 188214 | ICH-00257 | MF509984 | MF510095 | genseq-3 |
| | | ICH-00258 | MF509985 | MF510096 | GenSeq-3 |
| | | ICH-00260 | MF509986 | MF510097 | genseq-3 |
| | UF 190190 | ICH-01306 | MF510000 | MF510111 | genseq-3 |
| *A.* species | UF 190188 | ICH-01246 | MF509996 | MF510107 | genseq-4 |
| | | ICH-01253 | MF509997 | MF510108 | genseq-4 |
| | | ICH-01257 | MF509998 | MF510109 | genseq-4 |
| | UF 235990 | 2014-0301 | MF509933 | MF510044 | genseq-4 |
| | | 2014-0306 | MF509934 | MF510045 | genseq-4 |
| | | 2014-0315 | MF509935 | MF510046 | genseq-4 |